

The direct effect of CO₂ rise on the plant ionome

Implications for Exacerbating Global Malnutrition

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Abstract

Malnutrition is worsening, affecting every country and over 3 billion people. There is evidence that rising CO₂ levels will not only indirectly increase malnutrition through climate change effects, but also directly through a downshift in the plant ionome, reducing nutritional quality and increasing hidden hunger. Attempts to calculate the human health impact have been conducted with limited statistical power on a small group of nutrients. The impact on different age-sex groups, countries, and nutrients is still largely unknown. This research aims to fill this gap, creating a meta-analysis of the most data (5,809 entries), crops (43), and elements (31 plus phytate) of any study to date, resolving a methodological gap for disharmonious data and applying this to the GENUS model of global nutritional supply in 2011 for eight nutrients (calcium, copper, iron, magnesium, phosphorus, potassium, protein, and zinc) to see which countries will be able to provide enough nutrients for their citizens in a 550 ppm world compared to at 350 ppm.

Bootstrapping reveals a distinct 5% to 12% systemic downshift in the plant ionome. Both C3 and C4 plants respond, disproving the hypothesis that C4 plants are mostly unaffected by CO₂ rise and supporting the idea that the CO₂ saturation point is not directly linked to mineral uptake. Elements have a differential response, suggesting that the carbon dilution theory is an inappropriate explanation. Zinc, protein, and iron have the largest decreases, and zinc in chickpeas decreases the most (40%) of all groups. Grains (wheat and rice) and soybeans are the hardest hit crops, decreasing in nutritional value up to 12%.

The total nutrient supply decreases by 2.3% to 6.4%, increasing the malnourishment and obesity double burden. Countries will no longer provide enough nutrients from food solely due to changes in the plant ionome, impacting every country. Half of the world will develop new deficiencies. The strongest predictor of resiliency to nutritional changes from CO₂ rise is diet diversity. Exacerbating global inequality, the impact will be particularly pronounced in African and Asian countries, and among women aged 25-29 compared to men of the same age group and children aged 0-4 years. Changing plant stoichiometry will have dramatic global implications for hidden hunger, worsening or introducing deficiencies, especially in iron, phosphorus, potassium, and zinc.

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I dedicate this thesis to the 170,000 people living in the Netherlands with long Covid who are too sick to work. Whilst abandoned by the systems meant to support us, I will not let you be forgotten.

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Abbreviations

Acronyms

Notation	Description	Page List
aCO ₂	ambient carbon dioxide level	8
CAM	crassulacean acid metabolism	16, 30, 36, 53
eCO ₂	elevated carbon dioxide level	8
FACE	Free-Air CO ₂ Enrichment	5, 6, 10, 12, 15–17, 20
FAO	Food and Agriculture Organization	1, 33
FBS	Food Balance Sheets	34
FCT	Food Composition Tables	34, 35
GDD	Global Dietary Database	33, 34
GENuS	Global Expanded Nutrient Supply Model	2, 3, 32–36, 38, 54
IPCC	Intergovernmental Panel on Climate Change	2, 6
OTC	Open Top Chamber	5, 10, 15, 16, 20

Notation	Description	Page List
ppm	parts per million	1, 8, 13, 14, 18, 25, 26, 30, 32, 35, 39, 40, 42, 44, 45, 48, 51, 88, 89
RCP	Representative Concentration Pathway	2, 14, 35
RDI	Recommended Daily Intake	37, 38, 47, 49
SDG	Sustainable Development Goal	33
UN	United Nations	1, 32
WHO	World Health Organization	33, 34

1. Introduction

Motivation

Starting in the pre-industrial era, human activities have increased atmospheric concentrations of the greenhouse gas CO₂ from ~280 parts per million (ppm) to ~415 ppm, representing the most extreme increase in rate and amplitude of the past 3 million years (IPCC, 2022; Gojon et al., 2023). Since the turn of the millennium, the global CO₂ concentration has been rising by 20 ppm per decade (IPCC, 2022). We are living in the Anthropocene, an epoch marked by extreme climate change. We are also living in a time of global malnutrition. Although famine – a shortage of calories – is no longer as widespread as in decades prior, malnutrition – a shortage of nutrients – is increasing globally (World Health Organization, 2021). In 2014, 2.5 billion adults and 200 million children suffered from malnutrition, effecting every country. These numbers are quickly growing, and along with it, an epidemic of diet-related non-communicable diseases. By 2025, one in two people will be malnourished. Low-quality diets are the root cause of malnutrition, the largest global contributor to the global disease burden (UNSCN NEWS, 2017), and the leading risk factor for death (Afshin et al., 2019).

The Food and Agriculture Organization (FAO) of the United Nations (UN) identifies multiple causes and factors contributing to malnutrition, including climate change (FAO et al., 2022). CO₂ rise has an indirect effect on malnutrition through climate change by affecting the availability of food. Direct climate shifts such as rainfall variability, extreme weather events, temperature increases on land and in water, ocean acidification, and increased ozone levels affect food production. Biological consequences stemming from climate change, such as pollinator declines, greater postharvest losses, changes in primary production, and coral reef degradation further decrease food availability. Shifts in human socioeconomic systems, such as climate change-induced conflicts, lowered purchasing power, and price volatility further stress the food system (Myers et al., 2017; Giulia et al., 2020; Owino et al., 2022). The situation seems dire, but initial postulations of a positive effect of CO₂ rise on the predominant form of plants - those using a C3 photosynthetic pathway - promised hope. Growth in C3 plants is theoretically limited by available CO₂, dubbed the 'fertilization effect', and could possibly mitigate the increasing carbon dioxide rise through increasing primary plant biomass production. The increased yield was thought to be a positive effect of climate change since food production could increase

and feed more people (Dahlman, 1993). The effects this will have on aspects other than yield is less studied, but there is growing attention towards the direct effects of climate change on the nutritional value of food itself (Fanzo et al., 2018) thanks to the seminal papers by Loladze (2002, 2014b) and Myers et al. (2014). While the research is still sparse, considering the scale of the problem, the initial results are concerning; increasing atmospheric CO₂ concentrations can alter crop nutrient content. While plants grow more rapidly under higher CO₂ conditions, their protein and micronutrient content are lowered (Cotrufo et al., 1998; Fan et al., 2008; Fernando et al., 2012a; Idso and Idso, 2001; Loladze, 2014b; Myers et al., 2014; Seltenrich, 2017; Taub et al., 2008; Taub, 2010; Uddling et al., 2018; Ziska, 2022; Zhu et al., 2018), decreasing nutrient availability (Beach et al., 2019).

A diet that contains sufficient nutrient intake now could be a potentially poor diet health-wise in the future due to decreasing nutrient density in plant-based food. This begs the question: will these decreasing nutrient intakes be in crops that affect our daily intake to a significant degree? Further, who is affected by this, and how should our diets account for this information? Will countries be able to provide their people with enough nutrients in the future, or will the types and amounts of food need to change? These questions are still unanswered. While the evidence that increased CO₂ levels will decrease plant nutritional levels continues to mount, few studies have quantified this to a future model and extended this analysis to human health implications, and those that have were limited in their crops and nutrients analyzed. No analysis exists that unifies the existing data and analyzes a wide range of mineral micronutrients for edible crops representing all major food categories. This is an identified research gap (Ebi and Loladze, 2019). Thus, the direct impact of CO₂ rise on plant nutrition is unknown for most crops and nutrients. The extension of this - the impact this will have on malnutrition globally - is also unknown. This paper aims to bridge this knowledge gap.

Goal

The main research question is, *How will each country's dietary nutrient availability change in the future due to the direct effect of continued CO₂ rise on crop nutritional quality, and will it still be sufficient to meet the population's needs?* This is divided into two sub-questions addressed in separate chapters: 1) What is the effect of CO₂ rise on food crops?, and 2) What is the scale of the problem in the future? Which nutrients and countries are hardest hit? The first question is answered by a meta-analysis of existing research on elevated carbon dioxide levels and the plant's nutrient composition response. These studies are then categorized and analyzed in a way that retains sufficient power to create confidence intervals for likely future effects under a scenario similar to the Intergovernmental Panel on Climate Change (IPCC) end-century Representative Concentration Pathway (RCP) 4.5 in 2100 and IPCC mid-century RCP 8.5 in 2050. To answer the second question, we take these results and apply them as scenario models to the Global Expanded Nutrient Supply Model (GENuS) to analyze the theoretical differences in supplied nutrients per person per country, assuming no other changes in food procurement.

Structure

The report is constructed as follows: Chapter 2 discusses the development of ideas, notable papers, and their respective trends over time, concluding with a summary of the currently identified unfilled research gaps. The main body of the text is split into two chapters, one for each sub-question. They are split this way because the intended audiences for each part are overlapping, but divergent. Biologists and climate change scientists may be more interested in the direct effect of CO₂ on the crop ionome and less so in future scenario modeling of diets, while a public health specialist may wish to skip the modeling explanation and jump straight to the effect on human health in the second half. Of course, curious readers are welcome to read both chapters. Each chapter is written as a stand-alone article, but care was taken to avoid unnecessary repetition when read as one document. The plant ionome model is created and analyzed in Chapter 3 which uses linear models and bootstrapping methods to create confidence intervals of the nutrient levels of various crops in the future. These intervals are then applied to the GENU_S model in Chapter 4. This sketches a picture of the varying burdens countries will possibly have to bear. The implications of these parts and future research directions are synthesized and discussed in Chapter 5.

2 . Landscape Literature Review

1970s-1985: international mobilization setting a research agenda

The initial research into the fertilization effect took place in the mid-1970s, but by 1978 there was still no field data (BR Strain, 1978). In 1979, the American Association for the Advancement of Science asked for a research agenda on rising atmospheric CO₂ and climate change, leading to the 1982 International Conference on the Biological Effects of CO₂ on Plants (Dahlman, 1993). The conference pulled into question if the fertilization effect would hold in real-world conditions over a longer period, as most of the research thus far had been done under favorable short-term conditions. It was unknown how nutrient distribution would change, but it was already postulated that it could. Plant tissue physiology made it onto the short list of research objectives (Lemon, 1983).

Two years later, a comprehensive review covering over 1000 studies was published, saying "It also has been observed in studies that the food quality of some plant tissues declines as atmospheric CO₂ increases" (BR Strain and JD Cure, 1985, p. xvii). In the following 300 pages of writing, not once is a connection directly drawn between tissue nutrient changes and food nutritional values for humans. They highlight concern on the research gap between the effect of CO₂ enrichment and the needed minerals in the soil for optimal plant growth, calling it a 'high priority'. The flipside - the uptake of nutrients in plant tissues - was said to be an unknown as well, but this was given less attention in the proceedings and in the then-available literature. A large concern was the lack of models for global predictions on plant response to CO₂ to quantify the effect of stimulated growth (BR Strain and JD Cure, 1985, p. 47). Links were made between increased plant growth and increased agricultural productivity. Other chapters drew links between tissue nutrient changes and the effect on the soil and (non-human) herbivore populations. Additional studies in the same referred state "the net effect of elevated CO₂ is likely to be a decrease in nutrient availability and in the nutrient content of tissue. [...] We are far from having a predictive understanding of these effects in the various ecosystems. No long-term experiments with elevated CO₂ concentrations have determined the effects on these parameters"(BR Strain and JD Cure, 1985, p. 139). The need for a global model that takes nutrients into account was established, with discussions taking place on the optimal type of experiments and the costs they would require, but the concern for human health impacts appeared to be merely a passing thought.

1986-2002 'We don't know what we don't know': the hidden hunger theory

In the late 1980s technical accomplishments in Open Top Chamber (OTC) and Free-Air CO₂ Enrichment (FACE) technology spurred on further research, allowing scientists to conduct well-designed repeatable experiments in field situations (Dahlman, 1993). One of the first papers using this technology looked at the effect of long-term CO₂ exposure on nutrients in edible crops and showed a decrease in protein, carotenoids, and insoluble dietary fiber for sweet potato grown at elevated CO₂ conditions, although sensory evaluation scores didn't change from the ambient control (Lu et al., 1986). This is the first paper suggesting a 'hidden' change in food composition, although this is not explicitly stated by the authors.

A few years later, Tremblay et al. (1988) reported that CO₂ enrichment on celery seedlings led to a decrease of protein and mineral concentrations in the shoots. A smattering of papers about edible crops is published after that report, specifically on nitrogen and micronutrient changes due to CO₂ enrichment focusing on wheat (Conroy et al., 1994; Fangmeier et al., 1997, 1999; de La Puente et al., 2000), rice (Seneweera et al., 1996; Seneweera and Conroy, 1997; Ziska et al., 1997), radishes (Barnes and Pfirrmann, 1992; McKeen et al., 1996), tomato (Behboudian and Tod, 1995; Wheeler et al., 1997), barley (Manderscheid et al., 1995), lettuce (Chagvardieff et al., 1994), and cucumber (Segura et al., 2001). Some papers look at cofactors such as nitrogen and phosphorous fertilizer application. Fangmeier et al. (2002) publishes his work on potatoes, explicitly calling out the scarce research on the effects of CO₂ enrichment on nutrients other than nitrogen and phosphorus, and is the first to apply ozone as a cofactor for edible crops. The complex interactions are starting to be recognized and explored in meta-analyses (Cotrufo et al., 1998) which sometimes extend their results to potential effects on human and animal health (Idso and Idso, 2001).

The following year Loladze (2002) published a thought experiment suggesting that rising atmospheric carbon dioxide levels would lead to a globally imbalanced plant stoichiometry. It is the first paper that explicitly mentions 'hidden hunger' as a potential problem, saying that the reduced micronutrient intake for a global population with already sub-optimal intakes could become an 'enormous [...] problem'. At the time, scientists were suggesting that the micronutrient composition of plants was shifting purely due to 'carbon dilution', that is, that the proportions were only reduced due to a greater percentage of carbon in the plants. Loladze is one of the first to suggest that this may be an insufficient explanation. "All else being equal, this pattern would mean lower (nutritional value):(caloric value) of crops and the aggravation of the micronutrient malnutrition problem. It would also increase the imperative to breed rice, wheat and other staple crops with superior ability to concentrate essential elements such as Fe, Zn, I and Se" Loladze (2002, p. 459). Echoing the warnings of Fangmeier et al. (2002), he says, "The data are surprisingly scant. I hope that the scarcity and importance of the data will encourage the generation of new data on the changes in plant stoichiometry caused by a globally altered environment. It is startling that, among thousands of publications on doubled [CO₂], only one investigated its effects on the grain stoichiometry of rice, the world's most important crop" (Loladze, 2002, p. 460).

2002-2014: Meta-analyses ring the alarm bell

There is a small, but growing interest in the field. Thirty more papers were published in the following decade including meta-analyses (Taub et al., 2008; Taub, 2010), when in 2014 two seminal papers, Loladze (2014b) and Myers et al. (2014) are published. Loladze (2014b) presents a meta-analysis of 1,482 measurements of 7,761 observations of the effects of elevated carbon dioxide on 130 different species and cultivars and 27 elements pointing to a global systemic shift in the ratio between total non-structural carbohydrates and minerals, and that this ratio increase is greater than that of the carbon to mineral ratio in C3 plants. Rice and wheat are specifically mentioned as having reduced protein and nitrogen concentrations. This is the first dataset large enough to overcome the noise that previously obscured the effect of elevated CO₂ on the plant ionome, although two-thirds of the data is about non-edible plants and the statistical analysis power is insufficient to analyze the effect per element (Loladze, 2014a). He concludes that overall mineral concentrations will reduce by 8%, and this has the potential to increase the global challenge of hidden hunger and obesity.

Myers et al. (2014) publishes an analysis of a then-unpublished dataset by Dietterich et al. (2015) composed of 138 comparisons of edible crops from FACE experiments of six crops (corn, peas, soybeans, wheat, rice, and sorghum) for zinc, iron, protein, and phytate. His team found that elevated carbon dioxide was statistically significantly associated with significant zinc and iron concentration decreases for all C3 grasses and legumes. The link to the global challenge of zinc and iron deficiency is made, and selective crop breeding is offered as a potential solution. Myers et al. (2014) extends the dataset with 32 extra comparisons taken from literature, which further illustrates their conclusions. The message is clear: food nutrition will change due to climate change, and although the data is insufficient to predict exactly how, there is enough evidence that the results will be significant and not in our favor.

A limitation to both papers is that despite the large amounts of data, there was limited data and insufficient sample sizes to calculate with enough statistical power to distinguish the effect per element, and had too little data on crops besides wheat and rice. Loladze had a diverse dataset with 27 nutrients and less data available per food-nutrient combination meaning that it was not possible to split the dataset into smaller categories and draw conclusions about effects per element or crop. Myers had only 6 crops and only 4 nutrients and was still unable to calculate the results with enough power and significant values for all food-nutrient combinations. Understanding the effects of different factors was not possible with their datasets, but both highlighted the need for future research to better understand the effect on plants used for food.

2015-2023: Arrival on the international research agenda

Forty years after the first paper on this topic, alarm bells go off in large part due to the attention gained from Loladze (2014b) and Myers et al. (2014). Their work is the focus of award-winning news reports (Evich, 2017), the United States Global Change Research Program (USGCRP, 2016), and the United Nations IPCC

(IPCC, 2022). USGCRP (2016) listed further research on the impact of CO₂ rise on nutritional quality and needs as a priority in understanding how climate change will affect the health of Americans. In the following decade, 60 experimental results are published along with numerous meta-analyses and review articles. Some observe food crops in general (Medek et al., 2017; Uddling et al., 2018; Rajashekar, 2018; Soares et al., 2019; Toreti et al., 2020; Ainsworth and Long, 2021; Jayawardena et al., 2021; Semba et al., 2022), while others focus on groups such as grain and cereals (Al-Hadeethi et al., 2019; Ben Mariem et al., 2021), vegetable and legumes (Dong et al., 2018; Scheelbeek et al., 2018; Singer et al., 2020), and fruits, nuts, seeds (Alae-Carew et al., 2020) while others focus on specific crops such as rice (Chumley and Hewlings, 2020; Hu et al., 2021, 2022; Kumar et al., 2023) and wheat (Cakmak et al., 2010; Broberg et al., 2017; Wang and Liu, 2021).

Others extend the work, creating global models of potential deficiencies and effects on human health (Myers et al., 2015; Medek et al., 2017; Smith et al., 2017; Smith and Myers, 2018; Weyant et al., 2018; Beach et al., 2019). Giulia et al. (2020) systemically maps papers reporting on the influence of climate change on food nutrients, finding no empirical research focusing on CO₂ rise. Food nutrients and climate change are often only studied under the context of changing climactic variables such as seasonal, temperature, and precipitation variability. They hypothesize that this 'surprising' result of no papers on the topic could be because interdisciplinary work between environmental scientists and nutritionists is still nascent. They emphasize the need for empirical research, as opposed to the models that currently dominate the field.

The evidence that carbon dioxide rise affects the plant ionome is clear, but what that exact effect will be and how that will vary among crops is still poorly understood. Ebi et al. (2021) explores the research agenda, highlighting the numerous technological and knowledge gaps. Ziska (2022) recently published one of the clearest overviews of the state of research on rising carbon dioxide and its effect on nutrition, concluding the paper by saying, "We can and we must do better, not only in terms of [CO₂], plant and nutritional consequences, but in our ability to address the problem of anthropogenic climate change. If there is an unseen benefit to the current pandemic, ignoring public health consequences that can affect millions of lives is no longer an option. The evidence is here. Action is needed."

Pleijel and Högy (2015) published a paper calling the dilution hypothesis further into question based on a series of seven experiments. Several years later - and twenty years after Loladze (2002) first disagreed with the hypothesis - Ziska (2022) summarizes from multiple studies that this hypothesis is not supported by evidence. More theories are put forward: lower rubisCO or nutrient demand under elevated conditions, decreased photorespiration, the effects on stomatal aperture, and differences between transpiration-driven and diffusion-driven mass flow in plants. The sparse research on plants with a non-C3 photosynthetic pathway (CAM and C4) needs to be remedied to further support or refute some of these hypotheses. The mechanisms behind this differential response to in-

creasing CO₂ broadens an exciting field of research (Ziska, 2022; Kumar et al., 2023). What would be the effect on plants in a higher CO₂ world?

Present day: Unfilled research gaps and insufficient power

The questions asked previously remain unanswered, while other questions are accumulating. To the best of the author's knowledge, since Loladze (2014b) and Myers et al. (2014) published their meta-analyses, no new meta-analysis considers only edible food crops, analyzes more than just the nitrogen response, and includes all major food groups. Smaller analyses have been conducted for legumes, fruits, and vegetables (Scheelbeek et al., 2018), vegetables (Dong et al., 2018), rice (Hu et al., 2022; Kumar et al., 2023), wheat (Pleijel and Högy, 2015), and cereals (Ben Mariem et al., 2021; Broberg et al., 2017). A known research gap is the lack of harmonized input data for these models which makes it difficult to meaningfully compare different experiments (Toreti et al., 2020). Scheelbeek et al. (2018) standardizes the response rates linearly to the added CO₂. Broberg et al. (2017) looks at the relationship of added CO₂ relative to the adjusted baseline at 350 ppm using linear regression and concludes that for most elements a linear model has a better fit than a quadratic model. Pleijel and Högy (2015) calculated linear response functions per element. Limiting themselves to nitrogen, Medek et al. (2017), is the only author to use ambient carbon dioxide level (aCO₂) and elevated carbon dioxide level (eCO₂) as a modifier in linear models. The lack of harmonized inputs is still an unresolved research gap.

Other analyses, including Loladze (2014b) and Myers et al. (2014) which are used as the basis of models on the effects for human health (Myers et al., 2015; Smith et al., 2017; Smith and Myers, 2018; Beach et al., 2019; Weyant et al., 2018), aggregated the response rates without regard to the ambient, elevated, or added carbon dioxide levels. This paper aims to remedy this known knowledge gap (Toreti et al., 2020) by creating an updated database of CO₂ effects on all major edible food crops with available data, calculating estimated effect changes by taking the ambient and elevated CO₂ conditions into account, and finding a way of aggregating the data in a way that allows for sufficient power to apply in subsequent public health analysis. This improves the accuracy of the modeled results, extends their generalizability, and will try to shed light on the complex drivers behind the response rate variation. This resolves the two major problems with previous papers on the topic: insufficient statistical power and inconsistent experimental conditions. The following chapter deals with the creation of the updated database and exploration of the effect of rising CO₂ on the plant ionome. Later these results are applied to human diets in Chapter 4. The newly identified research gaps and suggestions for future research are given in Chapter 5.

3. Altered Crop Ionomes

3.1 Scope

This chapter is dedicated to extending existing meta-analyses to include more crops and nutrients, resolving the power issues and inconsistent experimental conditions, and analyzing these results in the context of each other, other models, and existing literature. This results in a model of the direct effects of increased CO₂ rise on the ionome of edible crops for humans. The implications on malnutrition are reserved for Chapter 4.

3.2 Methods

3.2.1 Database Creation

Combining known datasets

The logical place to start with creating an updated meta-analysis is to take the known existing databases: in this case, that is Loladze (2014a) and Dietterich et al. (2015) which was used in Myers et al. (2014). Their raw data was re-analyzed, and their calculated data from other research was recalculated and compared. This data was then filtered and combined.

The Loladze (2014a) dataset was filtered to the edible portions of the food crops, for a total of 37 articles. Each entry was checked, resulting in some changes (Appendix A.1). Only one article was not accessible for double checking the results (Cavagnaro et al., 2007). In total, this meant changing 41 entries and adding 245 entries. Combined with the filtering, the final dataset was 835 entries, excluding replicates.

The Dietterich et al. (2015) dataset was reprocessed, meaning that experiments were individually paired again, for a total of 1,608 entries. The minor changes to the dataset are shown in Appendix A.2. These pairs were used in Myers et al. (2014), and can thus be seen as a recreation of the Myers et al. (2014) which is not publicly available. Strangely, the results vary slightly between our results and his which are listed in his paper as 'Extended Data Table 1'. The 25 extra cited sources used in 'Extended Data Table 3' are referenced; ten are consulted by Loladze (2014b) and fifteen are unique to Myer's meta-analysis. However, only two of these sources contain accessible data (Conroy et al., 1994;

Seneweera et al., 1996), adding in a total of 18 entries. Between Loladze (2014a), Myers et al. (2014), and Dietterich et al. (2015), there are 2,462 entries.

To update the combined database for new articles published afterward and to find articles missed by Loladze (2014a) and Myers et al. (2014), a snowball search method is used. This method is chosen because for a second-generation literature review, it finds a comparable amount of literature as a traditional search, but is more time-efficient (Wohlin, 2016). This is done in two phases: forward and reverse.

Criteria for inclusion and exclusion

The search was conducted in October and November of 2023. Only journal articles written in English were examined. Inclusion criteria were edible crops grown at two or more CO₂ levels, direct measurements of one or more minerals at two or more CO₂ levels, and reported results given as either absolute concentrations or relative change. Reasons for exclusion were multi-generational tests, testing only non-edible (portions of) crops, exposing only a part of the plant to nitrogen, inconsistent or intermittent CO₂ application, super-elevated or uncontrolled levels of CO₂, and/or combined multiple factors per study where it was impossible to differentiate the direct effect of CO₂ (e.g. testing ambient CO₂ vs elevated CO₂ and ozone together). Papers that only looked at nitrogen were also excluded to keep the exclusion criteria in alignment with those of Loladze (2014b), but upon later reflection could also have been included. Only independent results are included, so if a paper recorded results at multiple time intervals for one experiment, only the latest results for the most mature plant parts are included. Multiple parts of the same plant are not included, and only the (most commonly eaten) edible part is included. These data inclusion rules allowed for the greatest variety of data while still keeping the entries independent.

Data processing

Data was taken from tables, text, or supplementary information where possible. If extracted from a figure, WebPlotDigitizer was used (Rohatgi, 2022). Ambient CO₂ levels were estimated using the Keeling Curve when they were not given by the study authors (Keeling and Keeling, 2017). Per entry, up to 26 pieces of (meta-)data are recorded, including the calculated delta and natural log of the response rate. This is summarized in Appendix A.3. Locations for FACE and OTC experiments were taken from the text when possible, and otherwise, the research institute's location was used.

Snowball search method

The forward method is the first phase; since Loladze (2014a), Myers et al. (2014), and Dietterich et al. (2015) are the seminal papers, it is logical to assume that most new papers would cite at least one of them. All papers citing at least one of the three papers are examined for inclusion. Once those were selected, any paper that was a review or meta-analysis was included in the second phase, which was a reverse snowball search. This is when the citations of the meta-analyses

and review papers were examined for further inclusion. This process was done iteratively until no new papers were identified (Table 3.1).

Table 3.1: Snowball search method results

Forward Snowball	Dietterich	Loladze	Myers
Articles citing	63	301	949
Journal articles in English	49	245	702
Kept based on title	25	68	164
Kept based on abstract	17	51	111
Kept based on skim	9	41	64
Total found (forward)	115		
Excluded duplicates	-30		
Excluded: failed to meet criteria	-38		
Articles included	47		
<hr/>			
Reverse Snowball (First Iteration)			
Review/meta-analyses examined	10		
New articles with relevant titles examined further	64		
Excluded: unlocatable	-1		
Excluded: not in English	-8		
Excluded: did not discuss minerals	-32		
Excluded: combined factors	-2		
Excluded: multi-generational	-1		
Excluded: review paper (no new data)	-1		
Articles included	19		
<hr/>			
Reverse Snowball (Second+Third Iteration)			
Article found via non-review article	3		
Articles included	3		
<hr/>			
Total new articles included	69		

The forward snowball search method was conducted using the LENS.org search engine. In total, 1,313 articles were examined and 85 were selected for database inclusion. Ten meta-analyses or review papers were identified by the forward snowball, and used in the reverse snowball: Alae-Carew et al. (2020); Ben Mariem et al. (2021); Doddrell et al. (2023); Dong et al. (2018); Hu et al. (2022); Kumar et al. (2023); Semba et al. (2022); Singer et al. (2020); Soares et al. (2019); Toreti et al. (2020). They collectively cited 65 new unique articles deemed

relevant based on their title, and after the exclusion criteria, 19 remained relevant for inclusion in the database. Pal Singh et al. (2008) was identified in a reverse snowball search by Semba et al. (2022), but its full-text could not be located. This has since been requested through ResearchGate. In the following reverse snowball iterations, Boufeldja et al. (2023) identified Almuhayawi et al. (2021), which identified Saleh et al. (2018). Beleggia et al. (2018) identified Singh et al. (2014). Several papers were only partially included because they did not supply their data in an accessible way (Jena et al., 2018), had missing supplementary information (Soares et al., 2019, 2021; Broberg et al., 2017), or hosted it on a now-defunct website (Köhler et al., 2019). These authors were individually contacted and asked to share their datasets. Only Köhler et al. (2019) responded, who graciously shared both their code and their dataset, and is thus included in the new database. Of the identified records by the search, 69 full-text articles with usable data were included in the database for a total of 3,348 new entries.

Total database

The total database currently has 5,809 entries from 109 articles. Each article contributes less than 2% of the entire database with the exception of Dietterich et al. (2015) [27.7%], Ujii et al. (2019) [7.0%], Köhler et al. (2019) [4.2%], Soares et al. (2019) [3.4%], Jin et al. (2019) [3.1%], Wang et al. (2020) [2.6%], Gao et al. (2021) [2.5%], Guo et al. (2022), Beleggia et al. (2018), and Heagle et al. (2003) with 2.1% each. The Dietterich et al. (2015) database is the compilation of six different studies in four countries. Had each study been listed separately, only the FACE experiments for wheat, rice, and soybeans would have been greater than 2% of the data, representing 12.4%, 6.4%, and 5.2% of the data respectively. Thus, even though the Dietterich et al. (2015) dataset represents a significant portion of the data, not one study or research group dominates the results, which reduces the chance for experimental bias. In terms of contributions per database, Loladze (2014a) contributes 14.4%, Dietterich et al. (2015) and Myers et al. (2014) collectively contribute 28%, and the snowball search method contributes 57.6% of the data.

To test for publication bias, the effect size was plotted against the number of replicates, to get the distribution of the effects (Egger et al., 1997). The resulting scatter plot (Appendix A.4) is funnel-shaped, wider at the bottom, and narrows as the sample size increases. The points are mostly symmetrical about the mean, with some outliers on the right-hand side. This suggests there is either no or possibly only a small amount of publication bias.

3.2.2 Response Rate Linearization

As identified in Chapter 2, the majority of meta-analyses and reviews suffer from two problems: too little power and a heterogeneous population. The first problem is potentially solved by combining multiple datasets and adding in the newly published data, as described in Section 3.2.1. The second problem has multiple possible solutions, but the one attempted here is the standardization of the dataset to a reference baseline and elevated CO₂ level. In this way, the varying

experimental conditions for the ambient and elevated carbon dioxide shown in Figure 3.2 are accounted for. This method assumes that the heterogeneity in responses is driven mainly by the variation in CO₂. Poorter et al. (2022) found that while plants have a CO₂ saturation point, studies looking at the effect of CO₂ rise on chemical composition, especially on minerals, show a linear response even above the saturation point. While there might be a saturation point, in the 200-1200 ppm range of the Poorter et al. study there is an observed linear response. It is possible that over a larger CO₂ range above 1200 ppm there is a 'true' saturation response, but those are conditions beyond the design of both their and our study. Of course, under high CO₂ regimes, it is more complex: higher levels are linked to higher temperatures, and precipitation rates, and how the plant reacts to this creates a complex interaction. However, for this study, it is a reasonable simplification to assume a linear response between mineral uptake and CO₂ rise at the range being considered. Some previous works have shown that for the tested levels, for most elements the response rate is roughly linear (Broberg et al., 2017). Scheelbeek et al. (2018) standardized the results to a certain level of added CO₂, while Pleijel and Högy (2015) used a linear response function based on a standardized baseline of ambient CO₂. With this precedent, and no overwhelming evidence to the contrary, we continue with an assumption of a linear response at reasonable levels of CO₂ increase, so that the data can be linearized. In the worst case, our estimate of the true effects is too conservative and is therefore still appropriate for further analysis.

The dataset records the delta, Equation 3.1, and the log response rate, Equation 3.2. The delta is defined as

$$\Delta = \frac{r_E - r_A}{r_A} = \frac{r_E}{r_A} - 1 \quad (3.1)$$

where

$$\begin{aligned} r_A &= \text{response at ambient CO}_2 \\ r_E &= \text{response at elevated CO}_2 \end{aligned}$$

A is the ambient CO₂ level, and E is the elevated CO₂ level. The natural logarithm is used as the effect metric to reduce the bias towards increases since the decrease is limited to 100% while the increase is theoretically unlimited (Hedges et al., 1999). It is defined as

$$\ln\left(\frac{r_E}{r_A}\right) \quad (3.2)$$

For clarity, let us refer to the adjusted ambient and elevated levels as A^* and E^* . To standardize the values to a given baseline, we need to first shift the response ratio from the ambient, A and elevated E level to the standardized baseline A^* and E^* , and then interpolate or extrapolate to the standardized elevated level G . To shift the response ratios to new levels of CO₂, shift both A and E by the same absolute amount so that A^* matches the baseline. The response ratio of

an experiment at $A=350$ ppm and $E=550$ ppm will have the same response ratio at $A^*=300$ ppm and $E^*=500$ ppm. The E^* value needs to be adjusted further to match the second target value for the elevated level G .

To bring the results for E^* linearly to the standardized elevated CO₂ level, defined as G , use linear interpolation which can also be used to extrapolate. The formula for linear interpolation, written in terms of the notation used, is as follows:

$$r_G = r_{A^*} + \frac{(G - A^*)(r_{E^*} - r_{A^*})}{E^* - A^*} \quad (3.3)$$

where

- r_{A^*} = response at adjusted/shifted ambient CO₂
- r_{E^*} = response at adjusted/shifted elevated CO₂
- r_G = response at goal/standardized elevated CO₂
- A^* = adjusted/shifted ambient CO₂ level
- E^* = adjusted/shifted elevated CO₂ level
- G = goal/standardized elevated CO₂ level

Plugging this into Equation 3.2 to calculate the response rate at the standardized baseline and elevated level which is used for all calculations after this yields

$$\begin{aligned} \ln\left(\frac{r_G}{r_{A^*}}\right) &= \ln\left(\frac{r_{A^*}}{r_{A^*}} + \frac{(G - A^*)(r_{E^*} - r_{A^*})}{(E^* - A^*)r_{A^*}}\right) \\ &= \ln\left(1 + \frac{G - A^*}{E^* - A^*}\Delta\right) \end{aligned} \quad (3.4)$$

The adjusted log response results can be converted back to delta percentage change using

$$\text{percent change} = 100 \times [e^{\ln(r_G/r_{A^*})} - 1] \quad (3.5)$$

For the following analyses a baseline, A^* , CO₂ level of 350 ppm is selected for two main reasons: one, 350 ppm is sometimes referred to as the last 'safe' level (Hansen et al., 2008) and secondly because it is within the range [310-455 ppm; average of 386 ppm] of the non-adjusted ambient CO₂ levels from the database. 360 ppm is the target constant concentration starting in 2200 of the RCP 2.6 (Meinshausen et al., 2011). The 'goal' elevated CO₂ level is standardized to 550 ppm. This is roughly the mid-century point for RCP 8.5 and the end-century point for RCP 4.5 and is where it will stabilize (Clarke et al., 2014; Meinshausen et al., 2011).

Outliers are detected by applying the inner-quartile method using a cut-off point of 1.5 IQR and 3 IQR relative to other data points in the same genus with the same tissue type (i.e. above ground, reproductive part, or below ground) and of the same element (Appendix A.5). Outliers are only excluded in a figure when explicitly mentioned.

Dataset Partitioning and Bootstrapping

The next step is to decide how to treat the dataset by calculating the average effect on the response variable, which is the natural log of the adjusted response ratio (Equation 3.4). While the effect for the entire dataset is calculable, it is interesting to calculate this for sub-groups to find possible drivers that explain the heterogeneity in responses. There are several possible drivers with recorded (meta-)data: between elements, C3 and C4 plants, experimental setups (i.e. FACE vs OTC vs pot vs chamber), plant parts (i.e. above ground stems and shoots, reproductive parts such as fruits and seeds, and below ground parts such as roots and tubers), and level of biological classification (e.g. family, genus, species). All possible drivers are included in the following analysis. Comparative boxplots and violin plots are used to compare possible aggregation levels, as well as guidelines from literature.

Analysis shows that the sample and subgroups are never normally distributed despite attempts at repairing this through outlier removal and log transformations, so a non-parametric method of analysis is used instead. Weighted bootstrapping with 10,000 replacements is used to calculate the 95% mean effect size confidence interval, the two-sided p-value with the null hypothesis being 'no effect', and the statistical power. The p-value is calculated by $p = \# [|Z^*| \geq |Z_{obs}|] / 10,000$ where # is the cardinality (Desgagné et al., 1998). Power is the chance the test will detect an effect size if present. The sample is shifted by the delta and then bootstrapped. The power is the fraction of these results that fall outside of the confidence interval for the original bootstrapped sample. The probability of a Type I error - a false positive - was set at $\alpha = 0.05$. This method is adapted from Loladze (2014b). When a sample is small, its variance can be much smaller than the population variance, which results in an overestimation of power. Using the estimate of the population variance instead, when larger, is the more conservative approach. For small samples less than 20, the larger of the sample standard deviation or the standard deviation of the entire dataset was used for calculations. This standard of using the greater of the two standard deviations for sample sizes less than 20 is chosen to remain consistent with the previous research done by Loladze (2014b). Both power and p-values are useful to analyze together because an experiment with a small sample size can have a significant p-value, but a low statistical power. Judging bootstrapped samples by both limits the analysis to powerful and significant results.

The whole dataset and several drivers are bootstrapped: element, study type, and C3 versus C4. Combinations are taken based on these results, resulting in dividing the dataset by C3 and C4, indoors (pot and greenhouse) versus outdoor (FACE and OTC) experiments, and element, and then bootstrapped by tissue type, family, genus, and species. Tunnel experiments are excluded due to their ambiguity; it is unclear how or where the experiments were conducted. The weighted dataset is used, so that experiments with more replicates have a higher chance of being (re-)selected during bootstrapping with replacement. The mean and 95% confidence intervals are transformed back from the adjusted log response to the percent change (Equation 3.5).

3.3 Results

3.3.1 Dataset Composition

The total database currently has 5,809 entries from 109 articles covering 32 elements plus phytate. In terms of nutrients analyzed, the most studied nutrients are also the nutrients that are common in deficiencies: zinc, iron, and protein followed by calcium and potassium (Kiani et al., 2022). Other common deficiencies such as calcium, magnesium, and copper (Biesalski and Jana, 2018) are also often included in studies. Zinc [9.3%], iron [9.3%], nitrogen [8.9%] as a proxy for protein, calcium [8.8%], phosphorus [8.7%], potassium [8.5%], manganese [8.2%], and magnesium [8.1%] are the most well-studied elements. They are followed by copper [7.4%], sulfur [5.2%], B [4.1%], phytate [2.8%], sodium [1.9%], molybdenum [1.3%], aluminum and nickel [0.9% each], and chromium and cadmium [0.7% each]. In order of decreasing number of entries, the following elements make up less than 0.5% each of the dataset: silicon, scandium, vanadium, bromium, strontium, selenium, lead, arsenic, cobalt, rubidium, chlorine, and barium. Regarding cofactors, 872 entries have temperature as a cofactor, 1,004 have irrigation, 732 have sowing time, 894 have phosphorous application, 1,932 have nitrogen application, and 244 have ozone application as cofactors.

Plants that use the C3 photosynthetic pathway make up 96.9% of the dataset. 90% of plants globally are C3 plants, and it is commonly believed that C4 plants are generally unresponsive to increasing CO₂ levels (Taub, 2010), which could explain why they are less studied. Plants following a crassulacean acid metabolism (CAM) photosynthetic pathway are unstudied, with a notable exception being the paper by Drennan and Nobel (2000). These plants, represented by pineapples, cactus fruit, nopales, and agave represent an extremely small portion of the global human diet and are left out in this meta-analysis.

FACE experiments make up 63.7% of the dataset, followed by OTC studies [15.1%], chamber [14%], greenhouse studies [6.8%], and tunnel experiments [0.5%]. FACE experiments provide the bulk of results for two reasons: 1) they are grown outside and thus have room for more samples and 2) they are prioritized for their more-accurate results because they are not limited by pot effects (Broberg et al., 2017; Ainsworth and Long, 2021). Crops such as wheat and rice grown under FACE conditions dominate the dataset, which is shown divided by family in Figure 3.1. That rice and wheat make up half of the dataset is logical; the most consumed crop worldwide is rice, and it is the primary staple crop for over half of the world's population. Another 2.5 billion people are dependent on wheat as their primary staple crop. Collectively, rice, wheat, and maize provide over 60% of the world's energy intake (Ebi et al., 2021). Corn, however, makes up less than 1% of the data, but this could be explained by its status as a C4 crop, which are believed to be non-responsive to increased carbon dioxide levels. FACE and OTC experiments are conducted in 15 different countries. Australia has the most experiments, providing data for 24% of all FACE-OTC experiments, followed by China (18.6%), the USA (18.3%), Japan (17.1%), Germany (9.4%), and India (8.2%). Africa, the Middle East, Eastern Europe, and Latin America are not represented.

There are 43 different edible crops representing 206 cultivars. Wheat and rice dominate the dataset, representing 27.7% and 25.8% respectively of all data points. In total, 59% of the dataset are grains in the Poaceae family which includes the 3% of the C4-based database. The next most commonly studied crop is the soybean which represents 16.5% of the data. Since 2015 legumes - primarily soybeans - are making up a larger portion of studies, which could be echoing a global shift towards more soy-based foods. The remaining 25% of the dataset are various C3 crops. They remain a small portion of studied crops, are typically studied indoors, and are not growing in interest as quickly as other crop types. This could be because they represent a wide diversity of plants that each make up only a small part of the human diet. These crops are members of 28 different genera contained in 8 Families: Poaceae [59%], Fabaceae [25.6%], Solanaceae [6.5%], Brassicaceae [3.4%], Asteraceae [3.0%], Cucurbitaceae [1.5%], Amaranthaceae [0.62%], and Apiaceae [0.52%]. Poaceae represents grains including wheat, rice, and millet. Fabaceae is the legume family. Solanaceae includes potatoes and tomatoes.

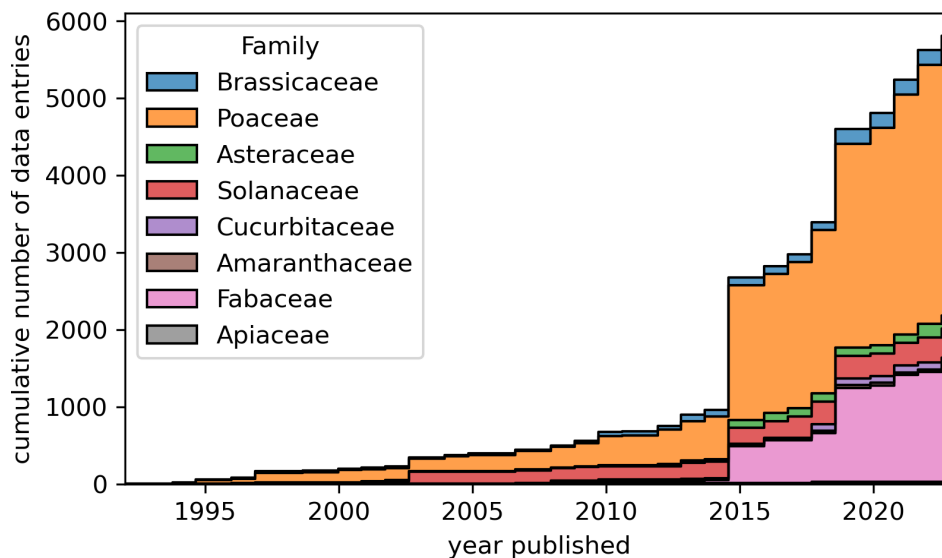


Figure 3.1: Growth of research on elevated CO_2 over time given as cumulative data published included in the database sorted by crop family.

3.3.2 Publications Over Time

While initially slow in growth, starting in the 2010s there is a relative increase in data published on the topic (Figure 3.1). It is also around this time that bigger datasets are published thanks to the larger FACE studies. There was a big jump in 2015 when Dietterich et al. (2015) published his dataset, which is to date the largest single contribution of any paper. Myers et al. (2014) only contributes two new articles to the database. While the snowball search method did identify papers published before 2014 not found or included by Loladze (2014a) and Myers et al. (2014), they do not represent a significant amount of data that could

skew their conclusions. In time, the data from the snowball method represents a significant portion of the dataset, covering new species and elements. The combined database is four times larger than the next largest database.

3.3.3 Experimental Carbon Dioxide Conditions

The studies were conducted at varying levels of ambient and elevated CO_2 (Figure 3.2). The effect of global carbon dioxide rise is already reflected in the ambient CO_2 levels shown in subplot a; earlier experiments were conducted at levels closer to 350 ppm while modern experiments are conducted at around 415 ppm. Subplot b in Figure 3.2 shows that there is also a variation between studies on amounts of CO_2 added, with peaks between 170 ppm and 200 ppm.

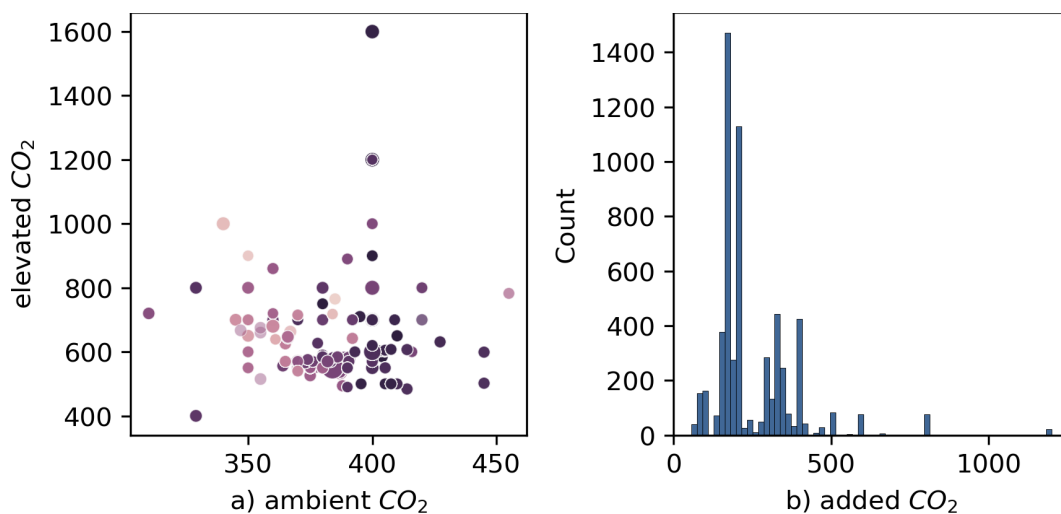


Figure 3.2: Experimental distribution of CO_2 levels in the database.

a) scatterplot of ambient versus elevated CO_2 levels and b) histogram of added CO_2 levels. For a) the dots are sized based on their total number of replicates and colored based on the year, where darker colors represent newer experiments and lighter colors represent older ones.

3.3.4 Bootstrapping Results and Drivers

In the low power range, power less than 0.4, there are wide confidence intervals, and these intervals get progressively smaller as power increases. The low-power regime is too noisy to show the effect of CO_2 rise, while the higher-power regions show the systemic shift in the plant ionome (Figure 3.3). Half of the bootstrapped results are in the high power regime and 77% of the combinations have a significant p-value less than 0.05. The dataset has a statistically significant ($p=0$) mean decrease of 3.6% (-3.4; -3.8). Of the significant results, chickpeas (*Cicer arietinum*) has the largest mean decrease of 40.5% and rubidium has the largest mean increase (28.2%) in C3 reproductive tissues.

Several drivers differentiate the responses (Figure 3.4). There is a clear difference between C3 and C4 photosynthetic pathway responses, where C3 plants

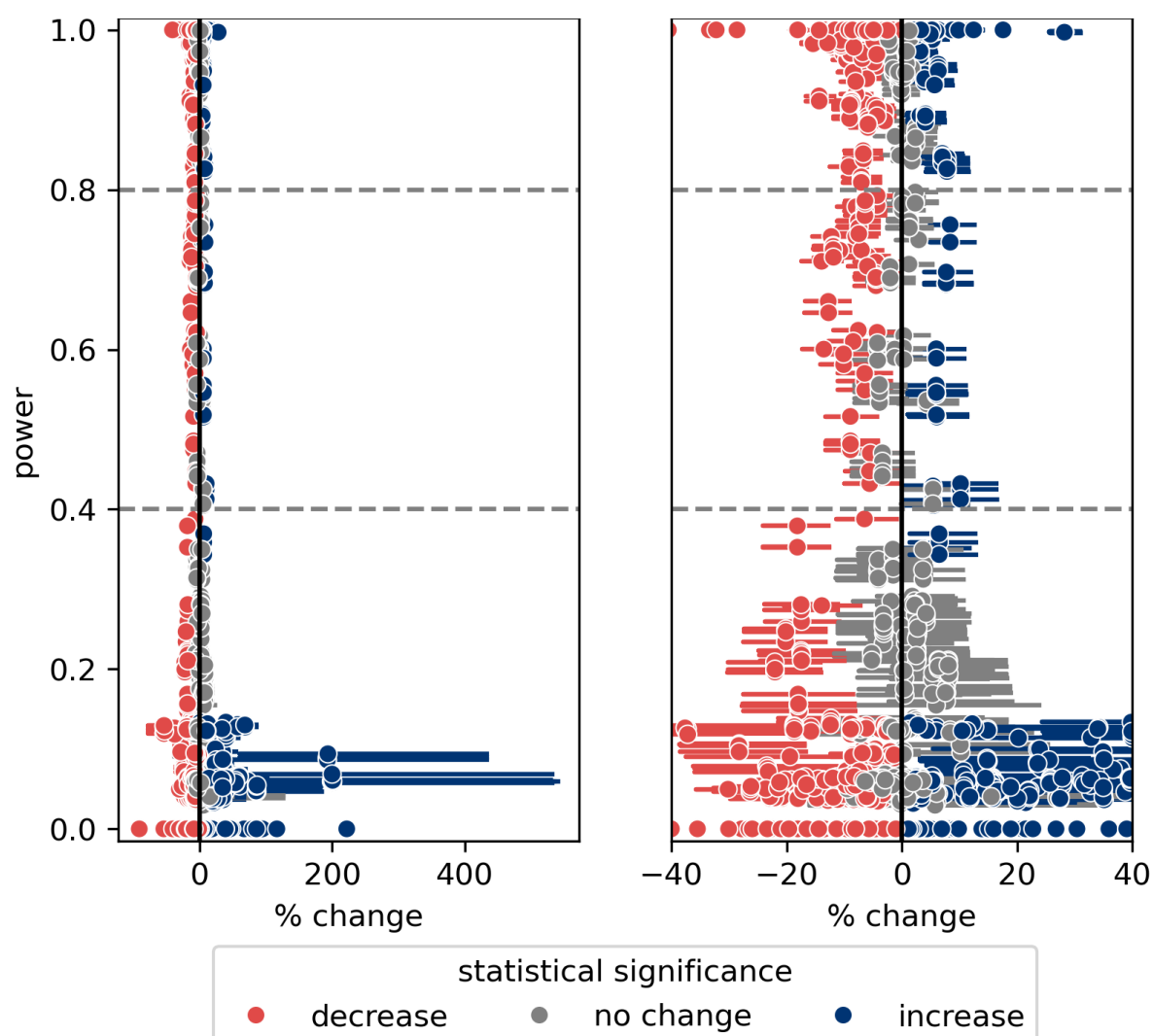


Figure 3.3: Bootstrapping results and confidence intervals for all classification divisions. The figure on the right is a zoomed-in version of the plot on the left to show the effect near $x=0$. All results are plotted as percent change versus their statistical power for the weighted bootstrapping results for the entire database, per photosynthetic pathway, element, tissue type, aggregated tissue type, and study type, as well as per element and outdoor/indoor study type grouping for these aggregations: C3/C4 type, C3/C4-tissue, C3/C4-family-tissue, family, family-tissue, genus, genus-tissue, species, and tissue. The lines denote the 95% confidence interval, and the dot denotes the mean. The significance level is determined at $\alpha = 0.05$. Dashed lines denote the divisions between the low (0-0.4), medium (0.4-0.8), and high (0.8-1) power regimes.

have a mean decrease, and C4 plants show no statistically significant change (Figure 3.4a). The type of experimental set-up matters, where outdoor OTC and FACE experiments show a larger decrease than indoor chamber experiments, and no change in greenhouse experiments (Figure 3.4b). FACE and OTC are not significantly different from each other, but both are different from chamber experiments, allowing them to be grouped as 'outdoor' experiments and chamber and greenhouse as 'indoor'. Elements respond differently, with 83% of elements with sufficient power showing a statistically significant change (Figure 3.4c). A comparison of C3 and C4 plants by element and study type is shown in Appendix A.6. The type of plant part analyzed also matters, where roots and tubers show the largest decrease. These plant parts show they can be grouped as 'below ground' (roots and tubers), 'reproductive' (grain, seed, fruit, pod), and 'above ground' (shoots and stems), and 'rice grain' (Figure 3.4d). Rice grains are separated due to their unique growing conditions. Tissue type is important, but differentiating between similar parts such as 'roots' and 'tubers' or 'grains' and 'seeds' does not yield better results. The main differences between tissues appear to be driven by the function it has in the plant. Since indoor experiments represent a minority of the data, contain no C4 plants, and are a better representation of true growing conditions (Broberg et al., 2017; Lieffering et al., 2004; Ainsworth and Long, 2021) for the following figures only outdoor experiments are shown. This is a loss of 24% of the data but improves the accuracy of the results. The indoor equivalents are shown in Appendix A.7.

There is a difference in elemental response between families (Figure 3.5) and species (Figure 3.6), with the main drivers appearing to be C3/C4 type, element, and tissue type. C4 plants have a less strong response than C3 plants in the same family, but in opposition to the common assumption that they have no response, there is a clear negative shift in nitrogen and zinc and a positive shift for boron. C4 plant sorghum has a 4% increase in potassium and no significant decrease for an average change of 0.5% across all significant minerals. For C3 plants, reproductive tissues tend to experience a stronger effect (-3.4%; CI: -4.7; -2.1) than the reproductive tissues for rice (-2.2%; CI: -4.0; -0.5) and this effect becomes more pronounced when split by families, with rice grains experiencing a third of the mean decrease that other C3 reproductive tissues experience in the Poaceae family, and C4 tissues experience no significant change. Reproductive tissues experience a milder effect than their underground counterparts (-4.4%; CI: -6.5%, -2.4%). The Solanaceae family has a similar decrease.

The Fabaceae family has a tempered average 2.6% decrease (-3.8; -1.5) which hides the variation between elements. Cadmium decreases by 20%, iron by 12.7%, and zinc by 12.2%, while aluminum (0.7%), nickel (11.7%), and rubidium (25%) increases. The Fabaceae family experiences a less severe decrease in nitrogen than other families, which is a result of their nitrogen-fixing properties. Between species in the Fabaceae family for all elements, *Cicer arietinum* has a stronger negative effect (-16.5%) than *Pisum Sativum* (-3.7%), which is more strongly affected than *Glycine max* (-2.8%), implying a species-specific influence.

Within the Poaceae family between species, wheat (*Triticum aestivum*) has a

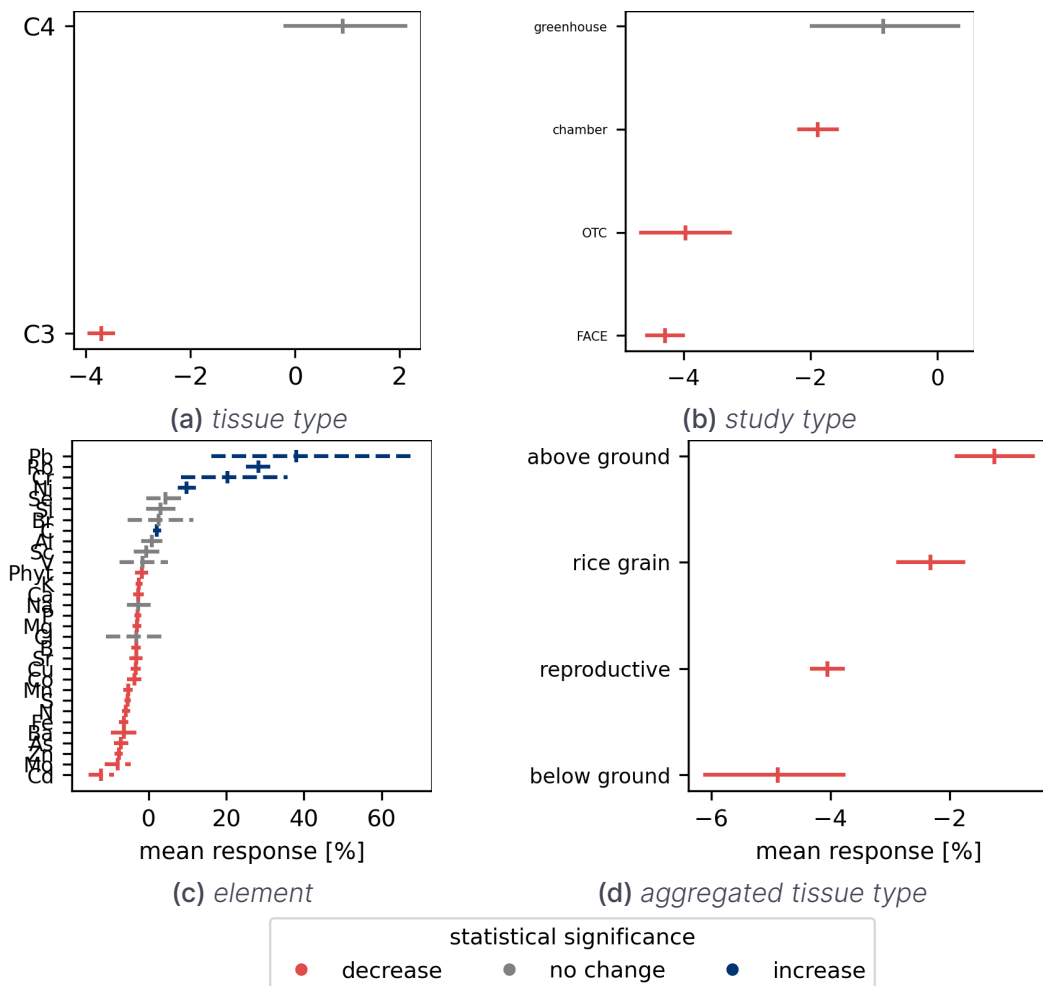


Figure 3.4: Bootstrapping results split by main drivers individually.

Values are given as percentage change for the dataset split by different drivers, given by the mean (tick) and 95% confidence interval (line) of the 10,000 bootstraps. Only results with power > 0.8 are shown and are color-coded by their statistical significance at $\alpha = 0.05$.

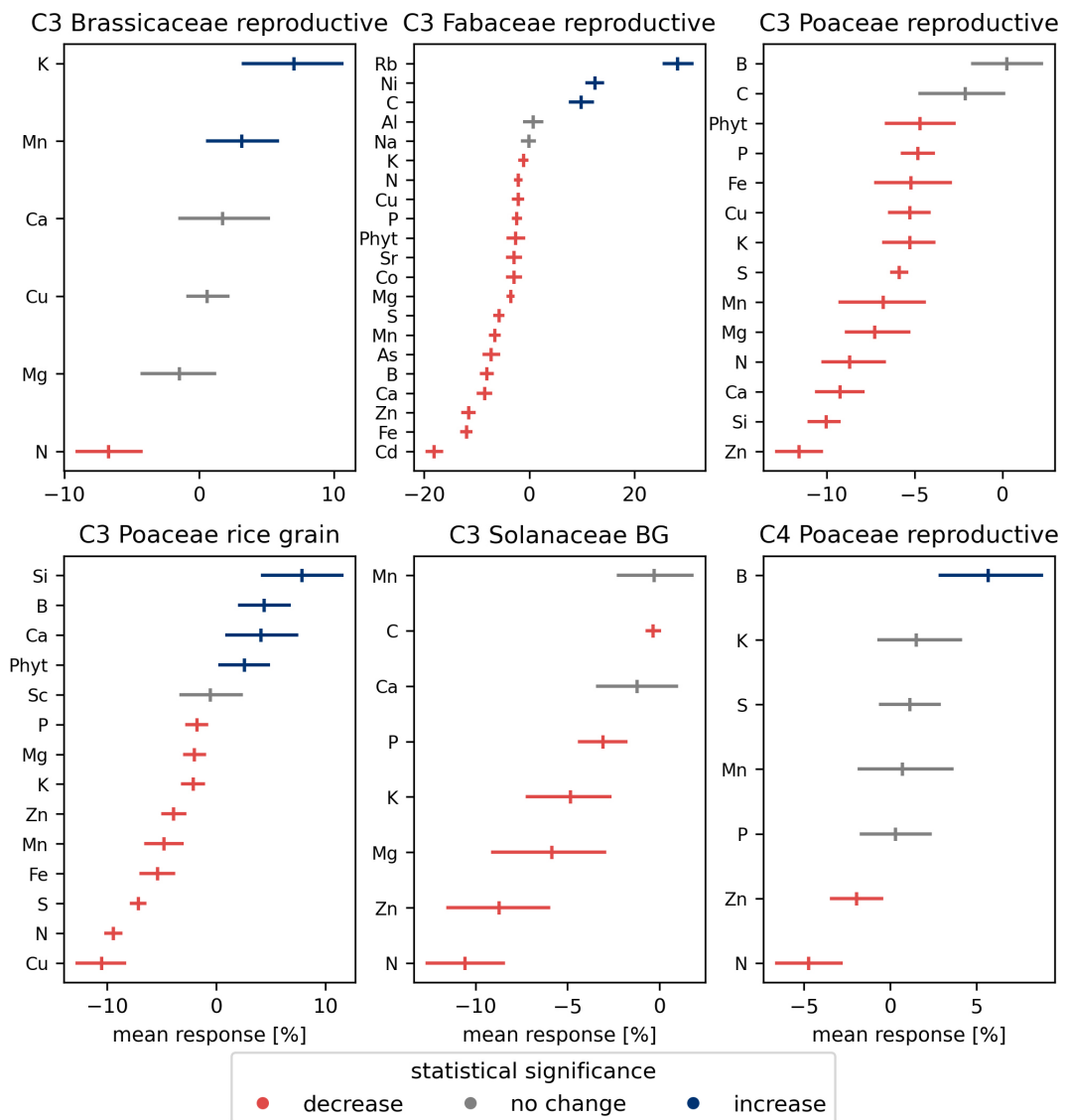


Figure 3.5: Bootstrapping results split by main drivers combined. Values are given as percentage change per element, sorted by photosynthetic pathway, family, and tissue type. The mean (tick) and the 95% confidence interval (line) are color-coded by statistical significance interpretation at $\alpha = 0.05$. Only results with sufficient power (>0.8) are shown. BG stands for 'below ground' and includes roots and tubers. Reproductive contains all fruits, seeds, grains, and pods. Rice grains are listed separately due to their unique growing conditions.

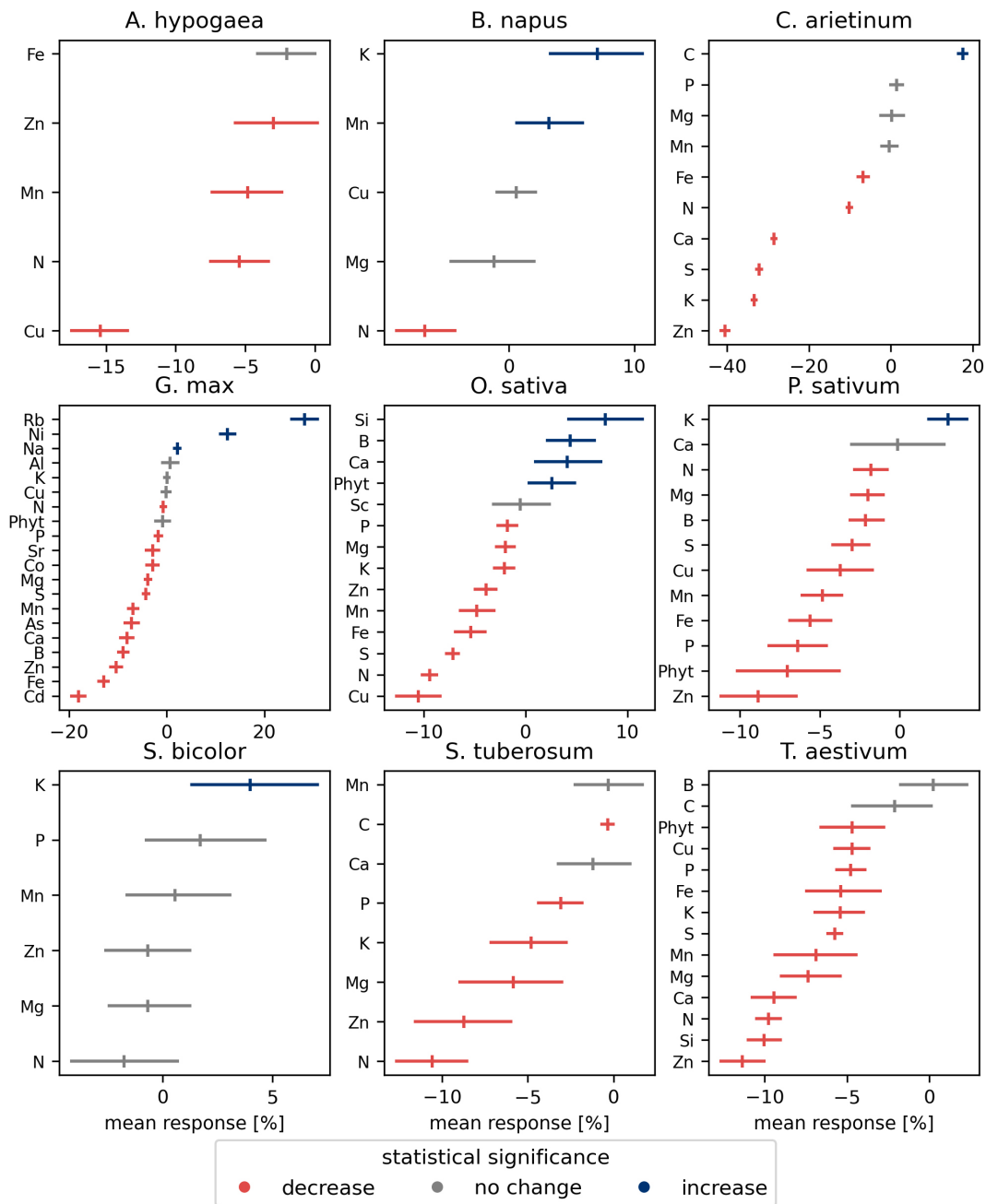


Figure 3.6: Bootstrapping results split by main drivers combined for important species. Values are given as percentage change per element, sorted by photosynthetic pathway, family, and tissue type. The mean (tick) and the 95% confidence interval (line) are color-coded by statistical significance interpretation at $\alpha = 0.05$. Only results with sufficient power (>0.8) are shown. All species are C3 plants except C4 plant 'S. bicolor'.

stronger negative impact (-6.5%) than rice (*Oryza sativa*, -2.2%), but per nutrient, the impact varies between -11.3% to -4.7% for wheat and -10.5% to 7.8% for rice. Both experience a 10% decrease in nitrogen and a 5.3% decrease in iron. Rice has a larger decrease in copper (-10.5% vs -4.7%) compared to wheat which has a stronger decrease in zinc (-4% vs -11.3%). Wheat has a 4.7% decrease in phytate, while rice has a 2.6% increase. Other species have an average element change of -6.5% for peanuts, a 0.5% increase for rapeseed, and a 4.5% decrease for potatoes.

3.4 Discussion

3.4.1 Dataset Partitioning

The data set is robust enough for splitting without a loss of statistical power, but using factors would have been a preferable method. Regardless of how the dataset was split into subgroups, the samples remained heteroscedastic. Removing outliers, while tempting, is difficult to justify without an understanding of the process mechanisms to determine what is a true outlier, and even the most liberal use of outlier removal is insufficient in creating a normally distributed sample. This limited the analysis possibilities. Bootstrapping was used to overcome the heteroscedasticity. Combining evidence from literature about expected differences in effects for certain drivers such as photosynthetic pathway, element, tissue type, and species was used to split the data into meaningful categories, but upon further reflection, an analysis method that could have used them as factors would have increased the analysis power. This should be a priority in future improvements to this work. Limited data samples mean that looking at cofactors such as fertilizer application is not yet possible to do in a meaningful way. They are left within the database in the hopes that they can be of use in the future.

Splitting by photosynthetic pathway yields interesting results, where both C3 and C4 plants show a negative shift in the ionome, with C3 plants being more strongly affected. Photosynthetic pathway type is thus most likely an important driver. This is discussed further below. There is also a differential elemental response, suggesting that CO₂ rise affects elements in plants in different ways, possibly owing to their different functions, and is thus also likely an important driver. This is also discussed further below. Tissue types also show differential responses ranging from 20% decreases and 25% increases in the same group, which is most likely linked to the elemental response and their different functions, and appears to be a driver as well. A physiological basis for the elemental differences in response rates has been suggested earlier in literature (Broberg et al., 2017; Ebi et al., 2021). Within the same family or genus, the tissue type had a large effect, and this is most visible in the Brassica genus, as in the dataset it contains 10 different species ranging from broccoli to oilseed, and has four different tissue types. The significance of the results did not improve by analyzing the species together. Even plants of the same photosynthetic type, tissue type, and element show different results, and this effect holds even for species within

the same family, suggesting a complex underlying mechanism. For every way of splitting, there is a trade-off between precision, power, and accuracy. Still, despite the multiple interactions, regardless of data splitting choices, the mechanism first shown by Loladze (2014b) holds: as statistical power increases, the systemic shift of the plant ionome becomes clearer.

3.4.2 Power Problems

The dataset overcame the statistical power issues others struggled with. While Loladze (2014b) calculated the power during the meta-analysis and calculated it was insufficient to partition the data into smaller groups, Myers et al. (2014) did not mention applying a similar analysis to their work but the sample sizes for some crop groups were small enough to assume that their work suffers from a similar limitation. The insufficient statistical power problem is most easily fixed by adding more data. Thanks to the influx of new papers on the topic (Figure 3.1) and the integration of the major datasets by Loladze (2014a) and Dietterich et al. (2015), the database contains almost four times as much data as originally analyzed. As the data availability increases, so does the power, meaning that the calculated result is more likely to represent the true effect. This illuminates the statistically significant shift of the plant ionome and provides better clarity on the magnitude and direction of the effect. For most nutrients, this means a decrease in nutrient uptake and availability. The power was calculated with a 5% effect size, but for many nutrients the effect size is even larger, suggesting a true higher power than what was calculated.

3.4.3 Experimental Conditions

Inconsistent experimental conditions are a complicated issue, which few authors have acknowledged or attempted to resolve. Both seminal papers, Loladze (2014b) and Myers et al. (2014), calculate if a p-value is significant for the log response compared to a null hypothesis of no change, and then took the average response change for all the tests by CO₂ level and response rate and reported it as percent change in mean concentration, regardless of cultivar/species, study type, baseline and elevated CO₂, amount of added CO₂, nor are the results weighted by the number of replicates in the experiments. An issue with this method is that it assumes one is looking for the mean in a population, but these are different test results run under different conditions, so they are not the same population. It is logical to expect - or at least test to reject the assumption - that there is a relationship between carbon dioxide parameters and response rate. Neither study tests this assumption to reject it. However, that they both achieve statistically meaningful results despite all sources of variation, suggests that if those factors are properly accounted for, the power and significance should increase even further. For Myers et al. (2014), the experimental conditions are similar enough to consider it a population, as the ambient CO₂ is between 363 and 386 ppm and elevated CO₂ was between 546 and 584 ppm. This means that the results reported in 'Extended Data Table 1' could be used as the average

percent change for the mean CO₂ levels. However, the analysis is then extended with other studies that have varying experimental conditions with elevated levels between 537 and 720 ppm. While in the Dietterich et al. (2015) experiments the average added CO₂ was 190ppm, in the experiments used to create the Extended Data Tables 2 and 3 this ranged from 150 to 360 ppm. So these are no longer comparable conditions for a population study, similar to the issue with the Loladze (2014b) analysis.

3.4.4 Response Rate Linearization

Although a conservative estimate, response rate linearization harmonizes the inconsistent experimental conditions despite concerns about the CO₂ saturation point, increasing statistical power and significance. Plant growth is limited by the available nutrients, including carbon dioxide. More CO₂ would result in more growth, up to a certain level called the 'carbon saturation point'. This point has been the subject of much research, trying to see if this limit in growth is also mirrored by limits in other physiological processes (Poorter et al., 2022). C3 plants have a CO₂ saturation point at 450 ppm while C4 plants have a lower saturation point at 360 ppm. C4 plants are already growing at their saturation point, and within a decade or two C3 plants will do so as well. In the dataset, there is a wider spread in measurements for C3 plants which is possibly driven by the larger variation in species and tissue types than for C4 plants. The average ambient CO₂ levels were 390 ppm and 379 ppm for C3 and C4 plants respectively. The elevated experimental level was 643 ppm and 583 ppm respectively, which is far above the saturation point for both types of plants. While C4 plants are generally less responsive to CO₂ rise than C3 plants, it seems logical to set the model to the saturation point and not the 550 ppm point selected earlier. Since the majority of experiments are conducted above 550 ppm, interpolation, and not extrapolation are used. If the nutrients did not change after the saturation point, meaning that their mineral saturation point is near their CO₂ saturation point, this would imply that our results are too conservative in estimating the effects of carbon dioxide increase on the C3 plant ionome. This is an underestimation of the effect, as this study design linearly attributes the effect between ambient and elevated levels, instead of between ambient levels and the saturation point.

For C4 plants, we expect to see no change, since both the ambient and elevated levels are above the saturation point, however, this is not what we see for some minerals. This is a curious observation that implies two things: 1) C4 plants are not as unresponsive to CO₂ rise as previously thought, and/or 2) the CO₂ saturation point is not directly linked to the mineral uptake saturation point, which has already been suggested by Poorter et al. (2022). With the precedent set by others for linearizing response rates and no evidence to the contrary, assuming a linear response at reasonable levels of CO₂ increase is an appropriate estimation for our purposes or in the worst case resulting in an overly conservative estimate of the true effects. This harmonization measure also addresses the research gap in data measurement disparity identified by Toreti et al. (2020).

3.4.5 Response by Photosynthetic Pathway

It is expected that C3 and C4 plants, owing to their separate photosynthetic pathways, would have different responses to elevated CO₂ levels, but the difference between the two is smaller than expected. Research suggests that C4 plants are less responsive than C3 plants, which are the predominant plant type globally (Cotrufo et al., 1998; Taub, 2010; Ziska, 2022). This assumption is reflected by the wealth of research into C3 plants, and comparatively sparse research done on C4 plants (Figure 3.1). Loladze (2014b) found no statistically significant effect for C4 plants and suggested that this is due to limited data unable to detect effect size less than 5%. The mean calculated effect for C4 plants is insignificant, however, the assumption that there is no effect is incorrect. On an elemental level, C4 plants show a significant decrease in nitrogen and zinc and an increase in boron. This could be a result of what others have also found: the carbon dioxide saturation point is not directly linked to the mineral saturation point (Poorter et al., 2022). C4 plants provide critical nutrients, and to assume that this will not change due to CO₂ rise is an oversimplification and disservice to countries with diets heavy on C4 plants such as corn and millet. It is perhaps time to rethink the assumption that C4 plants are immune to the effects of CO₂ fertilization and test experimentally if they too may reduce in nutrient quality over time.

3.4.6 Elemental Response and the Carbon Dilution Theory

Rice, potatoes, and wheat are harder hit than other species, while legumes and brassicas have more tempered effects. There is considerable response rate variation between elements of the same species. (Figure 3.5 and Figure 3.6). This pattern is also seen in Loladze (2014b) and in Myers et al. (2014), who reflected that this is inconsistent with the carbon dilution hypothesis. We see similar patterns across all three analyses: the elemental concentrations change in response to increased CO₂, but not in equal amounts. If the dilution hypothesis was the main driver for the shifting ionome, we would expect to see a uniform decrease among all elements. This decrease is not uniform among species, either, with some species being much harder hit for certain elements than others. Nitrogen fairs especially poorly among all plants except for those in the Fabaceae family, due to their nitrogen-fixing properties, but even within this family there are considerable differences in the nitrogen response between the chickpea, soybean, and field pea comparisons. This suggests that multiple factors are at play, or that the responsible mechanism works differently in different species. This finding supports the work of others who suggest that carbon dilution plays a part in a much more complex mechanism of changing plant stoichiometry and is a critical research gap (Soares et al., 2019; Ziska, 2022; Kumar et al., 2023).

3.4.7 Elemental Response and Health Impacts

Beyond furthering the understanding on a biological level, the elemental level differential response is worth investigating from a health perspective. Over half of the elements with sufficient power and p-values show a 5 to 12% decrease. For

critical nutrients such as protein, zinc, and iron, this can have devastating health consequences and contribute to further malnutrition, including in previously sufficient populations. It can also contribute to hidden hunger, where people consume enough calories but not enough nutrients. This effect is especially prominent for communities with a wheat, potato, or rice-based diet.

Biologists who are interested in minerals for plant growth often neglect to study minerals in plants that are only important for human health. Without their research, researchers focused on food lack the data they need. Critical nutrients such as zinc and iron receive the most attention, while non-critical nutrients are less likely to be studied, and in the case of some minerals, not studied at all. The changing stoichiometry is not yet predictable. Currently, the most studied elements are the ones critical for the plant or for human consumption, but this leads to a blind spot: what is happening to the minerals not needed for either group? Heavy metals such as lead showed an average 38% (16.1; 68.6) increase (p-val=0.0013, power=0.075). This is a low-power statement, so it is not a robust enough statement to draw a conclusion from, but it does hint at possible unintended shifts in the ionome with devastating consequences. This echoes what Ebi et al. (2021) stressed: although every chemical necessary for plants, is necessary for humans, the reverse is not true. Worse, elements that are benign to plants, can be toxic to humans and the shifting stoichiometry could shift these balances unfavorably. Micronutrients, such as iodine and selenium which are not always needed for plants, may be decreasing and this effect is not being sufficiently researched. In the case of phytate, which is an anti-nutrient, there is only data for certain species, but it does affect the absorption of critical nutrients. For toxic minerals, such as heavy metals, there are worrying experiments showing that they will increase, but there is too little data to say this with high confidence. Considering the large health effects an increased consumption of these minerals can have, they warrant significantly more attention than they receive.

3.4.8 Comparison with Literature

Myers et al. (2014) found a significant decrease in zinc and iron for all C3 grasses and legumes, as did our results, but the amounts differ. Our confidence intervals are narrower, and our mean is on average 1.5 times greater. The largest discrepancy is for iron in soybeans where they calculate -4.1% (-5.8; -2.5) compared to our -12.9% (-13.9; -12). Myers et al. had insignificant results for Glycine max (N), *Oryza sativum* (phytate), *Pisum sativum* (phytate), *Sorghum bicolor* (iron and phytate), *Zea mays* (nitrogen, zinc, and phytate) but our expanded dataset did have enough data to detect differences with a significant p-value. For the most part, our means are within 1.2 magnitudes of their means except for Fe in sorghum (9.3 times bigger), phytate in rice (2.1 times bigger), and protein in soybeans (1.4 times smaller). The large change is due to the addition of the results from Prior et al. (2008) which skews the mean upwards. Myers et al. also found no significant change in protein for C4 crops, while we found a 4.7% decrease (-6.6; -2.9). These results suggest that as the resolution and power increase, the measured effect remains either the same, or increases in magnitude, and

low-powered analyses could still be used as conservative estimates of the true effect.

Compared to Loladze (2014b), his calculated effect size of the dataset was twice as large, but this can be explained by the different composition of species. He calculated non-significant changes for manganese and potassium, while our dataset calculates a 6% and 3% decrease respectively. Among all elements, N declined the most for him (-15%; -17.8 to -13.1; $p < 10^{-5}$), but our calculated decline is only 5.8% and is superseded by declines in Cd, Mo, Zn, As, Ba, and Fe. Besides differences in methodology, this is also partially due to a larger dataset that contains plants with nitrogen-fixing properties and C4 plants that are less affected. This still supports the findings of Taub et al. (2008) of declining protein content, with similar results for rice and barley, and a more extreme decline (-10% vs -5%) for wheat. Similar to the results of Loladze (2014b), both indoor and outdoor experiments are robust and show a decline for most nutrients although they shift in magnitude. Loladze found a larger decline in indoor minerals, which he attributed to the higher CO₂ levels in the experiments. Having adjusted for these levels in our study, outdoor experiments often show a similar or increased magnitude change to indoor experiments per element and show a twice as large decrease overall.

3.4.9 Sparse Dataset

The dataset is rich enough to differentiate between nutrients even when splitting into smaller biological categories. This is an improvement to Loladze (2014b), who listed this as a research need. It also includes many more foods and nutrients than used in other meta-analyses (Loladze, 2014b; Myers et al., 2014; Pleijel and Högy, 2015; Broberg et al., 2017; Scheelbeek et al., 2018; Al-Hadeethi et al., 2019; Chumley and Hewlings, 2020; Ainsworth and Long, 2021; Ben Mariem et al., 2021; Hu et al., 2021; Jayawardena et al., 2021; Wang and Liu, 2021; Hu et al., 2022; Semba et al., 2022; Gojon et al., 2023; Kumar et al., 2023). Still, it is insufficient to analyze some key minerals such as magnesium, suggesting a discrepancy between research needs and what is measured, which is an identified research gap (Toreti et al., 2020).

Loladze also lists the lack of detail on major crops, "pertinent data are non-existent or very limited, including (in the descending order of calories provided to the world's population, FAO, 2013): maize (the top C4 crop), soybeans (including oil), cassava, millet, beans, sweet potatoes, bananas, nuts, apples, yams, plantains, peas, grapes, rye, and oats" (Loladze, 2014b, p. 9), and highlights this as a research gap. Ten years later, maize, soybeans, millet, beans, rye, and oats are now better studied with remarkable resolution improvements for (soy)beans, but the rest remain limited in data availability. It is not possible to say anything about the effects of the non-reproductive above ground plants, which have a unique nutritional profile and contribution to diets. Outdoor experiments neglect non-grain and legume plants, except corn. Comparisons between cultivars of these crops, except for rice and wheat, are also not yet possible. Caution is needed in extrapolating these results globally; the majority of the research is done in highly

industrialized countries, which biases the selected cultivars. People in Africa and Latin America may eat different cultivars, which could experience different responses. If this is the case should be investigated in future research.

3.5 Conclusion

The newly enlarged database containing 105 articles and 5,809 entries covering 31 elements plus phytate provides enough evidence to confidently say that there is a systemic shift in the plant ionome due to the direct effect of CO₂ rise from 350 ppm to 550 ppm. This shift is evident across different data splitting choices and increases in magnitude and precision as different drivers are accounted for. Significant elevated CO₂ response variation drivers include photosynthetic pathway, element, tissue type, and biological classification. Both C3 and C4 plants show a negative shift for most elements, with C3 plants having a larger magnitude. Tissue types also have an effect, most likely related to their different functions in the plant. Elements respond differently as well, which probably also has a physiological basis, with nitrogen fairing the worst among all plants except for legumes, and zinc and iron also fairing poorly. This result calls the carbon dilution theory further into question.

Considerable variation in magnitude among species in the same family regardless of the same photosynthetic pathway and tissue type suggests that the underlying mechanism affected by CO₂ rise is complex. These complex interactions suggest that a multi-factorial model would have been more appropriate than splitting the data. This would have improved the power, but more importantly, given more insight into which drivers have the largest effect. Still, as statistical power increases the plant ionome shift becomes clear.

The dataset is large enough to overcome the power problems other authors faced in their meta-analyses, but still, critical data is lacking, which is a commonly cited research gap. Little is known about CAM and C4 plants, non-grain plants, and non-critical nutrients in all crops. The level to which the dataset can be split and remain powerful enough depends on the crop type, with significant results for staple crops rice, wheat, potatoes, peas, soybean, and chickpeas. Rapeseed, peanuts, and sorghum are also able to be analyzed for certain elements. While some non-grain plants are powerful enough on the family level, more data is needed on non-grain plants and C4 plants. More data is needed on elements other than iron, nitrogen, and zinc in all species. More data is also needed on (cultivars of) staple crops grown and consumed in non-highly industrialized countries. Foods commonly eaten in Africa and Latin America are largely left out of experiments, and non-grain plants often eaten in Asia are not studied either.

The response rate linearization is a conservative approach to solve disharmonious model inputs and is preceded by other meta-analyses, revealing that C4 plants are not as unaffected by increased CO₂ levels as previously thought. Considering the carbon saturation point, which relates to plant production, the nutrient response rate continues to be affected at higher levels suggesting that they are not at the same point. If this were true, our calculated results would be

a conservative underestimate of the true effect. Still, we see that C4 plants do respond to elevated CO₂ levels despite the ambient level already being above their saturation point, suggesting that these two points are not identical. That C4 plants show a shift also calls into question the assumption that C4 plants are not affected by CO₂ rise, which would imply that more research needs to be done on the direct effect on C4 plants. They are currently understudied but provide critical nutrients by way of corn, millet, and sorghum.

Zinc, protein, and iron have large decreases, and most elements show a 5 to 12% decrease, which has dramatic implications for the nutritional content of food and can contribute to malnutrition and hidden hunger. Communities with a wheat, potato, or rice-based diet will experience larger impacts than those based on non-grain diets. Often critical nutrients for plant growth or human health are studied, which has led to a blind spot. Non-critical nutrients such as heavy metals or phytate show some signs of an increase, but because they are not well-studied, it is not possible to draw any confident conclusions. Non-essential elements for plants that are toxic to humans could be increasing in plants, and this effect is not being measured. The ionome is not necessarily downshifting for all nutrients, and since the elemental response varies, it is critical to understand how the complete picture of plant stoichiometry changes to carbon dioxide will look, or else we have to bear the unintended consequences of a shifting ionome with potentially devastating health consequences. Multi-generation experiments are also needed - multi-generation experiments are not included in this database, and are too few to be used as their own database. Once we understand what the effects of increased CO₂ are on plants, we need to move on to a better understanding of the long-term effects. There is evidence to suggest that this will be different than the single generation changes (Lemon, 1983; Li et al., 2019).

Comparing the results to other known datasets shows results of similar magnitude, but smaller confidence intervals. This suggests that the analysis method is appropriate. As the resolution and power increase with the addition of data, the measured effect often remains the same or increases in magnitude, suggesting that low-powered analyses are still possibly useful as conservative estimates of the true effect.

4 . Nutritional Availability

4.1 Scope

The implications of the nutritional changes modeled in Chapter 3 are examined in this chapter, whose goal is to calculate the change in theoretical nutritional availability supplied per country for three different age-sex groups in a 350 ppm versus a 550 ppm CO₂ world. This is done by applying the model from Chapter 3 to the GEnUS model of food availability and comparing the change for the elements zinc, iron, calcium, phosphorous, potassium, magnesium, and copper as well as for nitrogen as a proxy for protein.

4.2 Introduction

Human bodies need both adequate intake and ratios of macronutrients (fat, protein, and carbohydrates) and micronutrients (e.g. vitamins and minerals) for smooth functioning and development. Macronutrients deliver energy and key building stones for the body, while micronutrients run the processes. For short periods, macronutrients can be substituted for each other in the body. Micronutrients, in contrast, cannot be substituted for each other, and cannot be made by the body, so they must be consumed through one's diets or supplements. When one's micronutrient intakes are inadequate, despite sufficient calorie intake, the term 'hidden hunger' is used (Biesalski and Jana, 2018). Both long-term shortages of critical macronutrients and micronutrients are a concern. The extended effect of cognitive and physical deficiencies are not just isolated to the malnourished person through lower educational attainment, participation in the workforce, and poorer overall health outcomes, but impact the entire society through slowed economic growth, increased healthcare costs, loss of GDP, and an intergenerational cycle of worsening poverty (European Parliament, 2014).

The UN System Standing Committee on Nutrition have labeled our failing food system as a "planetary problem on the scale of HIV/AIDS, tobacco and now climate change [...] Malnutrition has re-emerged as a major public health problem. Since diets are modifiable risk factors, we can modify them" (UNSCN NEWS, 2017). Poverty and malnutrition amplify each other, which "increases health care costs, reduces productivity, and slows economic growth." This is the impetus for the UN Decade of Action on Nutrition from 2016-2025, led by

the World Health Organization (WHO) and the FAO. It sets targets in the Agenda for Sustainable Development by 2030, linking Sustainable Development Goal (SDG) 2 (end hunger, achieve food security and improved nutrition and promote sustainable agriculture) and SDG 3 (ensure healthy lives and promote well-being for all at all ages) (World Health Organization, 2021).

The FAO identifies multiple causes and factors contributing to malnutrition, including climate change (FAO et al., 2022). While originally analyzed with the understanding that climate change will reduce food availability through decreasing amounts of arable land, reduced biodiversity, and changing weather patterns (Giulia et al., 2020; Owino et al., 2022), there is a growing amount of attention for the direct effects of climate change on the nutritional value of food itself (Fanzo et al., 2018) thanks to the seminal papers by Loladze (2002, 2014b) and Myers et al. (2014). The combined effects of climate change will cause a decrease in nutrient availability (Beach et al., 2019). While plants grow more rapidly under higher CO₂ conditions, their protein and micronutrient content are lowered (Cotrufo et al., 1998; Fan et al., 2008; Fernando et al., 2012a; Idso and Idso, 2001; Loladze, 2014b; Myers et al., 2014; Seltenrich, 2017; Taub et al., 2008; Taub, 2010; Uddling et al., 2018; Ziska, 2022; Zhu et al., 2018). Zinc, iron, and protein deficiencies are the main identified nutrient-related risks of rising CO₂ levels, with an estimated hundreds of millions of people expected to be placed at risk of a deficiency and a worsening of deficiency in the two billion people already suffering from it. Countries already struggling the most with malnutrition will be disproportionately affected (Myers et al., 2017; Beach et al., 2019; Medek et al., 2017; Smith et al., 2017). A diet that contains sufficient nutrient intake now could be a potentially poor diet health-wise in the future due to decreasing nutrient density in the food. The question becomes, will these decreasing nutrient intakes be in crops that affect our daily intake to a significant degree, who is affected by this, and how should our diets account for this information?

4.3 Methods

4.3.1 Justification

Determining dietary food and nutrient intake on the individual level in populations is notoriously difficult (Micha et al., 2022). Issues in data collection, reliability, harmonization, and public availability have precluded a representative global model of dietary intake (Passarelli et al., 2022). There have been many attempts at resolving this, including through the creation of the Global Dietary Database (GDD) (Miller et al., 2021), the DELTA model (Smith et al., 2021), and nutriR (Passarelli et al., 2022). The best tool depends on the goal (Serra-Majem et al., 2003). The model used in this paper is called GENUS for theoretical nutrient supply. Since it is unknown if on a country level, enough nutrients are available now and in the future, it is better to look at theoretical food availability, and not actual consumption. The actual food availability is limited by losses in storage and transport, spoilage, unequal distribution, and poverty. Using theoretical availability means we look at how much food is imported or grown in a country

and what is possibly available in an ideal system with no waste or inefficiency. The theoretical availability determines if a country can supply its inhabitants with enough nutrients under a better-optimized food system. If a country is unable to supply enough nutrients with equal distribution and zero losses, then it will not be able to supply enough nutrients with unequal distribution and system inefficiencies. This means that the estimates calculated here are conservative, and most likely more people are affected than what the model determines. This study also does not include the indirect effect of climate change on the production or availability of food. Future forecasting of food supplies is fascinating but beyond the scope of this work.

4.3.2 Bridging GENUS

GENUS is a global model which covers 152 countries comprising 95.5% of the global population to estimate the dietary supply of nutrients (Smith et al., 2016). It estimates nutrient availabilities for 225 food categories for 34 age-sex groups using Food Balance Sheets (FBS), the GDD, and regional Food Composition Tables (FCT). The dataset covers calories, macronutrients, 11 vitamins, and 8 minerals: Ca, Zn, P, Cu, Na, K, Mg, and Fe. GENUS provides information on supplied food, not true consumption, so the results should be interpreted as a best-case consumption scenario, assuming no losses from spoilage or waste and no gains from locally grown or gathered foods.

Three datasets from GENUS are used in this research. The first, 'Nutrient Supplies by Food and Country (2011)' (Smith, 2018c) is a series of datasheets, one for each nutrient. Each sheet stores the median and the 95% confidence interval of nutrients supplied per food per median person per day per country. From the second dataset, 'Edible Food by Country and Year' (Smith, 2018b), only the latest year - 2011 - is used. It contains a matrix of the median and 95% confidence interval of the amount supplied per food per median person per day per country. The nutrient content per gram of food, NC, in each country in 2011 is calculated by

$$NC = \frac{\text{'Nutrient Supplies by Food and Country (2011)'}}{\text{'Edible Food by Country and Year'}_{2011}} \quad (4.1)$$

The last dataset, 'Edible Food by Age and Sex (2011)', has the same structure as the previous dataset but is separated by age-sex group (Smith, 2018a). Multiplying the calculated nutrient content, NC, with this dataset calculates the daily supply of nutrients, NS, per food per person in each age-sex group per country in 2011.

$$NS_{2011} = NC \times \text{'Edible Food by Age and Sex (2011)'} \quad (4.2)$$

To constrain the analysis, three age-sex groups are selected from GENUS for analysis: children 0-4 of both sexes, women aged 25-29, and men aged 25-29. These groups are selected for several reasons. Young children and pregnant women are both part of the WHO nutrition targets (Global Nutrition Report, 2021). Women during the pre-conception phase must consume enough nutrients, or

these deficiencies will be passed down to their fetuses. Women between 25 and 29 are taken because that contains the global median age of women's age at birth of their first child in 2011 (United Nations, 2024). Men of the same age group are taken as a comparison for gender-based differences. For children, the first 1,000 days from conception to their second birthday are critical in terms of brain development. Deficiencies developed in this time are largely impossible to reverse at a later stage, with lifelong cognitive and physical deficiencies as a result (Biesalski and Jana, 2018).

The daily nutrient intake results calculated by Smith (2018d) are slightly larger than what we calculate using their work. Smith used Monte Carlo simulations of different nutritional food profiles to estimate the total nutrient range and reported this as the median and 95% confidence interval for the country's intake and per age-sex group. We combine the median food intake per country with the median nutritional content per country calculated from GENUUS using Equation 4.1 and then use Equation 4.2 to adjust this to the intake per age-sex group. For this reason, our results for total nutrient intake per age-sex group are not perfectly aligned. A more complex analysis that uses both the median and confidence interval of the bootstrapped model from Chapter 3, the GENUUS food intake, and the nutritional content of the food would provide more robust results, but this is not possible without receiving the inputs for the Monte Carlo simulation from Smith.

4.3.3 Adding in the Changing Plant Ionome

The bootstrapped ionome model from Chapter 3 is applied to the GENUUS data to calculate nutritional supplies under a current scenario and a future scenario based off of the 2011 food supply composition. For the current intake, a 350 ppm world is used, although this is lower than the current CO₂ level (Keeling and Keeling, 2017). This is selected because 350 ppm is viewed as the last 'safe' level (Hansen et al., 2008) and is only 10 ppm below the target constant concentration starting in 2200 of the Representative Concentration Pathway (RCP) 2.6 (Meinshausen et al., 2011). The future scenario is at 550 ppm which is roughly the mid-century point for RCP 8.5 and the end-century stabilization point for RCP 4.5 (Clarke et al., 2014; Meinshausen et al., 2011). The 2011 dietary supply is held constant between the scenarios and does not reflect changes in food availability.

We limit both databases to the overlapping minerals and protein as proxied by nitrogen. The sodium coverage is insufficient in the GENUUS database, but because most people consume the majority of their sodium through added salt, and not directly from plants, it is excluded as well (Smith et al., 2016). Although the GENUUS database has limited information on magnesium due to lack of coverage in three of the six FCT, it is still worth adding in as it is a common deficiency (Kiani et al., 2022). The final examined nutrients are zinc, iron, calcium, phosphorus, potassium, magnesium, and copper as well as nitrogen as a proxy for protein.

We look at minerals and not at calories and fat for several reasons: 1) A shortage of macronutrients on a short-term scale can be substituted by other macronu-

trients, while micronutrients can not be substituted for each other. 2) It is highly unlikely that one has insufficient macronutrient intake but sufficient micronutrient intake. 3) The effect of macromalnutrition is more easily apparent, while micromalnutrition is insidious. The 'hidden hunger' malnutrition phenomenon is growing (Biesalski and Jana, 2018). Protein is included, despite being a macronutrient, because it affects the nutritional requirements for calcium, magnesium, and zinc (World Health Organization and Food and Agriculture Organization of the United Nations, 2004).

Not every food in the GENUS database is included in the ionome database, so a conversion table is created. The table categorizes the GENUS food groups as a nut/seed, fruit/vegetable, legume, cereal, fat, corn, sweetener, rice, wheat, meat/seafood, dairy, eggs, or miscellaneous. Each was then categorized as having a possible change or not. Any food of animal origin including all dairy, eggs, meat, and seafood, was listed as having no change, as well as 'Sweeteners; other', 'Mushrooms and truffles', and 'Miscellaneous + (Total)'. Those that could change under the changing plant ionome model had the following metadata listed: tissue type of the most commonly eaten part of the plant, photosynthetic pathway (left blank when multiple answers are correct), and as possible per aggregation level the Family, Genus, and Species it belongs to.

A compromise between high-statistical power data subsets and samples reflective of the foods they are modeling is needed. Per GENUS food category with a potential change the following hierarchy is used to assign it to a bootstrapped sample of its respective element, based of its biological classification (species, genus, family), tissue type, and photosynthetic pathway (C3 or C4): species → genus-tissue pair → C3/C4-family-tissue pair → family-tissue pair → C3/C4-tissue type pair → tissue type → C3/C4 type → whole dataset. The minimum group size is selected as the one with the highest level of differentiation while still having an adequate group size for bootstrapping. This group size is then input in the changing ionome model, and using the bootstrapping hierarchy is bootstrapped with 10,000 times per GENUS food category and element. These results are then converted back from the adjusted log form to a percentage change.

A minimum group size of 16 is selected (Figure 4.1). All element-food pairs are high-powered (statistical power > 0.8), and 98.7% have a significant p-value ($\alpha = 0.05$). The only way to increase the power is to dramatically increase the level of aggregation, which is not worth the loss of refinement per food. The aggregation levels allow us to keep crucial crops represented as species for rice and soybean for all elements, potatoes for most elements, and wheat on the genus level. Soy, potatoes, and rice are analyzed on the species level, and wheat on the genus level. Legumes are analyzed on the C3 Fabaceae family level. Corn and other grains are analyzed on the C3/C4-family-tissue level. Most vegetable-element pairs are analyzed on the C3/C4-tissue level and vegetable shoots and tubers and mixed vegetables on the C3/C4 level. Only fermented beverages (C3 and C4), mixed grains (C3 and C4), and pineapples (CAM, i.e. not C3 or C4) were analyzed on the tissue level. Due to their mixed C3/C4 status with no common

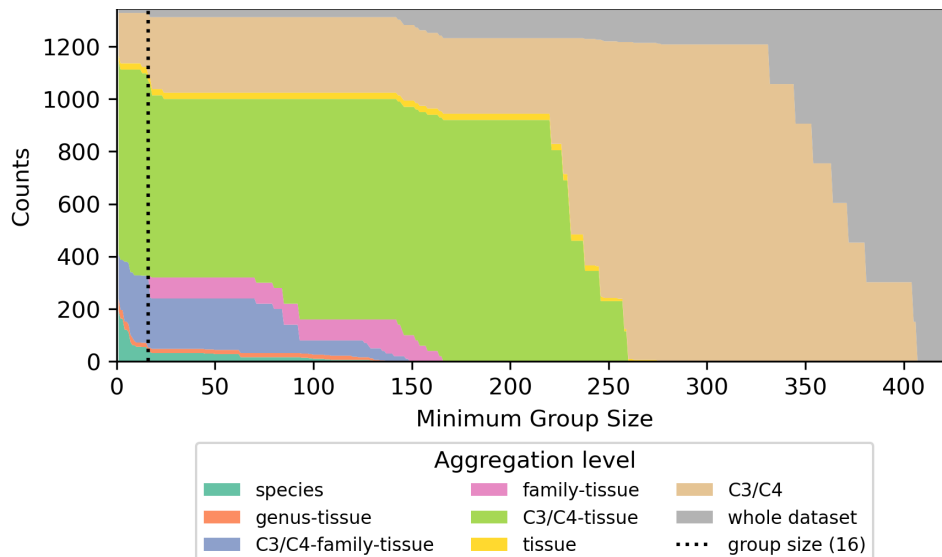


Figure 4.1: Aggregation levels used per group size for all food-element combinations. Only plant-based foods are shown. Our selected minimum group size (16) is denoted with a dotted line.

tissue, alcohol, and sugar used the entire dataset as a proxy.

4.3.4 Minimum Nutrition Requirements

The Evolution of RDIs

Determining a set of minimum necessary nutrition requirements is a field wrought with debate. Those already malnourished, ill, or with high levels of activity will have different needs than the standard population. Different countries have different meanings and intentions for a Recommended Daily Intake (RDI), divide their population into different segments, determine adequacy with a different metric, and have different available and preferred foods which have their own uncertainties regarding nutritional composition. Compounding this uncertainty is that there is insufficient data to determine human requirements. The first RDI was determined in 1862 to figure out the cheapest way to buy just enough food to avoid 'starvation-disease' in the unemployed (The United Nations University, 1982). It was only in 1913 that the concept of a 'vital amine' originated, and in 1926 it was isolated (Mozaffarian et al., 2018). In 1933 they were used to avoid declines in labour productivity during the depression. It wasn't until World War One that this became a matter of national security, determining the energy requirements "to feed the army and nation" (The United Nations University, 1982). The League of Nations, US, and UK independently created standards presented for the first time in 1941. In the 1960s countries started fortifying their foods, and by the 80s were modifying RDIs to also prevent chronic illness. The focus on reducing world hunger in 1990 was successful, but by 2010 the focus shifted to the double burden of hidden hunger (Mozaffarian et al., 2018). Meanwhile, malnutrition levels are rising again globally (World Health Organization, 2021), and the intention of the RDI is still not unified.

Selecting RDIs

Today, there is still debate on which bio-markers are relevant, how nutrients interact, and how to unify the diversity of diet-risk pathways. In lieu of a better, easily applicable option, this study takes the reductionist approach to determine malnutrition levels by using RDIs, and interactive effects are not taken into account. For calcium, iron, magnesium, and zinc, the RDIs are taken from World Health Organization and Food and Agriculture Organization of the United Nations (2004). For zinc and iron, all levels of bioavailability are considered. A country is only considered deficient if they have not enough supply for any level of bioavailability. A country that drops to a different level of bioavailability is not per se considered to be deficient, but the drop is noted in the model. For potassium, copper, and phosphorus, the adequate intakes are taken from the US NIH (National Institutes of Health Office of Dietary Supplements, 2022b,a, 2023). Recommend protein intake is taken from Richter et al. (2019). The RDI classification is consistent with GENUs classification for men and women between 25-29, so the values could be extracted directly from the table. The nutritional intake needed for a non-pregnant woman was used and is thus a conservative estimate for the needs of the average woman. For children, the RDI classification does not match the GENUs classification because the RDI varies significantly throughout the first few years of life. The RDI applied to GENUs is the weighted RDI value from literature by age. For example:

$$RDI_{0-4} = 0.1 \times RDI_{0-6 \text{ months}} + 0.1 \times RDI_{7-12 \text{ months}} + 0.6 \times RDI_{1-3 \text{ years}} + 0.2 \times RDI_{4-6 \text{ years}} \quad (4.3)$$

The RDIs are weighted equally by the needs of breastfed children and children fed by other methods. These RDI inputs (Appendix B.1) are compared with the results of the bootstrapping.

4.3.5 Diet Resiliency

There is ample debate on what it means to have a sustainable diet. Three identified challenges for growth in the food system are the rising population, improving economic conditions, and changing climate. As personal income rises, people tend to buy more meat and dairy (Finley et al., 2017). With this in mind, it is interesting to examine if wealthier countries, proxied by their GDP per capita, have a tempered effect from CO₂ rise. This examination is done by scatterplots. Countries with the largest and smallest decreases are also examined in terms of diet composition.

4.4 Results

4.4.1 Nutritional Insufficiencies at 550 ppm

Children 0-4 years

Children from birth through four years of age have the smallest change in dietary supply, with only 30 countries developing a new supply shortage or increased

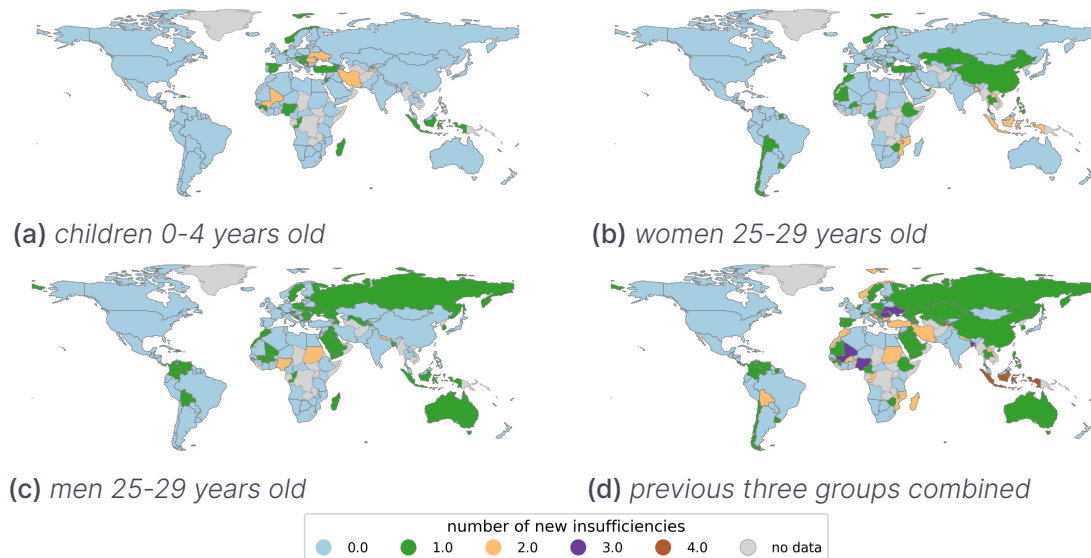


Figure 4.2: Number of new nutrient (Ca, Cu, Fe, Mg, P, K, N, Zn) deficiencies due to the effect of CO₂ rise on plant composition in a 550 ppm world versus a 350 ppm world, assuming a 2011 dietary supply composition.

required bioavailability need, primarily in iron and zinc. Increased bioavailability levels mean that the diet is only sufficient under a certain context and that these needs have become higher. Four countries experience two new deficiencies (Iran, Mali, Romania, and Tajikistan) (Figure 4.2a), while the rest of the countries experience one or no new deficiencies. Accounting for existing insufficiencies only 18 countries can supply enough food for children 0-4. Three of these countries are in Asia (Armenia, Palestine, and Syria), one is in North America (Canada), Oceania (New Zealand), and South America (Uruguay). The remaining 12 are in Europe (Albania, Belgium, Belarus, Denmark, Estonia, Greece, Ireland, Italy, Lithuania, Montenegro, Netherlands, and Poland).

In a 550 ppm world, young children will not have a significant change in dietary supply of protein, copper, or magnesium availability due to CO₂ rise. Much of the world's children have an insufficient calcium supply, and Turkey joins this group at 550 ppm. Tajikistan is the only country that becomes phosphorus and iron deficient for its children, although more countries experience a higher required iron bioavailability need. Fifteen countries (Austria, Bosnia and Herzegovina, Cyprus, Dominican Republic, Grenada, Croatia, Indonesia, Iran, Montenegro, North Macedonia, New Caledonia, Nigeria, Norway, Romania, Serbia, Slovakia, Tajikistan, and Ukraine) will experience an increase in required bioavailability levels of iron. Ten countries (Armenia, Congo, Georgia, Guinea, Hungary, Iran, Madagascar, Mali, St. Lucia, and the Netherlands) will experience an increase in required zinc bioavailability levels, which could mean insufficiency depending on the dietary context. Children in seven countries (Israel, Jordan, Luxembourg, Mali, Romania, Spain, and Ukraine) will have a higher risk of potassium deficiency, joining about half of the world's children who are already deficient (Figure 4.3).

Women 25-29 years

Since most countries already have an insufficient supply of iron for women aged 25-29, fewer countries (35) develop a new deficiency or increased required bioavailability requirement than for men (40) (Section 4.4), primarily in zinc and magnesium (Figure 4.3). Six countries (Bangladesh, Benin, Indonesia, Laos, Mozambique, Sri Lanka) have two new deficiencies, while 29 countries (Bolivia, Bulgaria, Burkina Faso, Cameroon, Chile, China, Costa Rica, Croatia, Djibouti, Ethiopia, Gambia, Kazakhstan, Latvia, Mauritania, Moldova, Morocco, Norway, Palestine, Philippines, Portugal, Suriname, Switzerland, Tajikistan, Thailand, Trinidad and Tobago, Turkey, United Arab Emirates, Uruguay, and Zimbabwe) experience one. When accounting for existing insufficiencies, only Palestine has enough theoretical nutrients available for women 25-29 at 550 ppm.

The majority of countries do not supply enough calcium to young women, and at 550 ppm, Kazakhstan joins them. Young women will remain sufficient in copper except in Suriname and Tajikistan. Protein supplies will be insufficient in eight countries (Bangladesh, Djibouti, Indonesia, Laos, Mozambique, Sri Lanka, Thailand, and Zimbabwe). Globally, women are insufficiently supplied with iron in very few countries, including all of Europe, South East Asia, North America, and South America. At 550 ppm, Benin and Mozambique will have too little iron to meet the needs of women. A few countries in Africa and Asia will continue to have sufficient iron in the future, while five countries (Benin, China, Mozambique, Palestine, and Turkey) will have sufficient iron but only under a higher bioavailability diet. Globally most countries can provide enough zinc, but fourteen countries (Cameroon, Chile, Costa Rica, Ethiopia, Gambia, Mauritania, Benin, Laos, Latvia, Switzerland, Portugal, Sri Lanka, the Philippines, and Morocco) will have higher required zinc bioavailability needs. Trinidad and Tobago joins Tajikistan in having a phosphorus deficiency. Three countries (Burkina Faso, Norway, and the United Arab Emirates) will be unable to supply sufficient potassium, which is already found in parts of South America, Africa, and Europe and commonly throughout Asia. Magnesium supply will become insufficient in seven countries (Croatia, Bangladesh, Bolivia, Bulgaria, Indonesia, Moldova, and Uruguay) joining the predominantly southeast Asian countries that already have a dietary supply shortage.

Men 25-29 years

Men aged 25-29 experience the greatest change in nutritional supply, with 40 countries developing a supply deficiency or a higher required bioavailability requirement (Figure 4.2c), primarily affecting the supply of iron and zinc (Figure 4.3). Men in Nepal, Nigeria, and Sudan experience two new deficiencies, while other countries have only one or no new ones. Accounting for existing deficiencies, 27 countries will still be able to supply enough nutrients for men aged 25-29. Five are in Asia (Armenia, Kazakhstan, Palestine, Syria, and Turkey), two in North America (Canada and the United States), and one in Oceania (New Zealand) and in South America (Uruguay). The remaining 18 are in Europe (Albania, Austria, Belgium, Belarus, Denmark, Estonia, France, Greece, Ireland, Italy, Lithuania, Luxembourg, Latvia, Montenegro, Netherlands, Poland, Portugal, and Romania).

No country will have newly insufficient copper or phosphorus supplies. Three countries (Haiti, Congo, Tajikistan) will have insufficient protein supplies. Sudan will have a calcium supply deficiency. Eighteen countries (Austria, Azerbaijan, Bangladesh, Bulgaria, Cyprus, the Dominican Republic, Grenada, Indonesia, Jamaica, Korea, Madagascar, Mali, Montenegro, Nigeria, Nepal, Romania, Ukraine, Uzbekistan) will have increased iron bioavailability requirements. Two countries (Tajikistan, New Caledonia) have insufficient iron under any requirement. Ten countries have increased zinc bioavailability requirements (Belgium, Estonia, Iraq, Luxembourg, Nigeria, Panama, Poland, Sudan, Sweden, Yemen). Nine countries (Australia, Bolivia, Bosnia and Herzegovina, Burkina Faso, Morocco, Nepal, North Macedonia, Russia, Saudi Arabia) will have newly inadequate potassium supplies. Three countries (Brunei, Colombia, Venezuela) will have insufficient magnesium.

Table 4.1: Number of countries affected by the percentage change in nutrient supply given as the mean and 95% confidence intervals.

		Countries Affected [#]	minimum [% change]	mean [% change]	maximum [% change]
Ca	m/f 0-4	1 (1; 1)	0.6 (0.7; -1.1)	2.6 (3.2; 1.9)	6.4 (7.4; 5.4)
	m 25-29	1 (2; 1)	0.5 (0.6; -1)	2.5 (3.1; 1.8)	6.2 (7.2; 5.3)
	f 25-29	1 (1; 0)	0.5 (0.6; -0.9)	2.5 (3.1; 1.8)	6.3 (7.2; 5.3)
Cu	m/f 0-4	0 (0; 0)	2.4 (2.8; 1.9)	3.9 (4.8; 3.1)	6.6 (8; 5.3)
	m 25-29	0 (0; 0)	2.3 (2.8; 1.8)	3.9 (4.7; 3)	6.5 (7.8; 5.2)
	f 25-29	2 (2; 0)	2.3 (2.8; 1.8)	3.9 (4.7; 3)	6.5 (7.8; 5.3)
Fe	m/f 0-4	17 (22; 15)	2.4 (3.2; 1.6)	5.7 (6.9; 4.4)	8.8 (9.9; 7.7)
	m 25-29	17 (19; 13)	2.2 (2.9; 1.5)	5.6 (6.7; 4.3)	8.8 (9.8; 7.7)
	f 25-29	5 (9; 9)	2.5 (3.2; 1.6)	5.7 (6.9; 4.4)	8.8 (9.8; 7.7)
Mg	m/f 0-4	0 (0; 0)	2.9 (3.6; 2.1)	4.6 (5.8; 3.4)	6.7 (8.2; 5)
	m 25-29	3 (3; 1)	2.8 (3.5; 2)	4.6 (5.8; 3.3)	6.7 (8.2; 4.9)
	f 25-29	7 (10; 5)	2.8 (3.5; 2)	4.6 (5.8; 3.3)	6.7 (8.2; 4.9)
P	m/f 0-4	1 (1; 1)	1.2 (1.4; 1)	2.4 (2.9; 1.9)	4.1 (4.9; 3.4)
	m 25-29	0 (0; 0)	1.1 (1.3; 0.9)	2.3 (2.8; 1.9)	4.1 (4.9; 3.3)
	f 25-29	1 (1; 1)	1.1 (1.3; 0.9)	2.4 (2.9; 1.9)	4.1 (4.9; 3.3)
K	m/f 0-4	7 (9; 5)	1.9 (2.6; 1.1)	2.8 (3.9; 1.8)	4.3 (5.7; 3.1)
	m 25-29	9 (12; 4)	1.8 (2.6; 1.1)	2.8 (3.9; 1.8)	4.2 (5.9; 3)
	f 25-29	3 (3; 3)	1.9 (2.6; 1.2)	2.8 (3.9; 1.8)	4.2 (5.9; 3)
N	m/f 0-4	0 (0; 0)	2.3 (2.6; 2.1)	4.9 (5.5; 4.3)	8 (8.7; 7.4)
	m 25-29	3 (4; 3)	2.1 (2.3; 1.8)	4.7 (5.2; 4.1)	7.9 (8.6; 7.2)
	f 25-29	8 (9; 9)	2.2 (2.5; 1.9)	4.8 (5.4; 4.2)	8 (8.7; 7.3)
Zn	m/f 0-4	9 (10; 7)	2.9 (3.2; 2.6)	6.4 (7.1; 5.7)	10.1 (11.1; 9.1)
	m 25-29	10 (11; 8)	2.6 (2.8; 2.3)	6.1 (6.7; 5.4)	10 (11; 9)
	f 25-29	14 (17; 14)	2.8 (3; 2.5)	6.3 (6.9; 5.6)	10.1 (11.1; 9.1)

4.4.2 Comparing Countries Across Age-Sex Groups

Globally all countries will struggle to supply enough nutrients to all three age-sex groups (Section 4.4), except for Palestine, assuming the dietary supply composition is held constant in a 550 ppm world. All other countries have at least one insufficient supply for at least one age-sex group. Compared to children and young men, young women have the most deficiencies in the most countries and nutrients. Men have sufficient nutrients in relatively more countries than women and children do, although this is only a relative success. 119 new supply deficiencies or increased required bioavailabilities will arise (CI: 146; 100) going from a 350 ppm to 550 ppm world. At 550 ppm, 80 countries will develop one or more new supply deficiencies on top of any existing supply deficiencies (Figure 4.2d). Of these countries with new nutrient supply shortages or increased required bioavailability requirements for sufficiency, 40 will not supply enough nutrients for men 25-29 years of age, 35 will not supply enough nutrients to women 25-29, and 30 countries will not supply enough nutrients from children 0 to 4 years of age. North America is the only continent with no new deficiency or changed required bioavailability needs for food supplies for all three age-sex groups. Indonesia and Tajikistan will face the largest amount of newly insufficient supplies, with four new deficiencies each, and are the only countries that develop at least one new deficiency for all three examined age-sex groups, although the deficiencies are not in the same nutrients. Bangladesh, Mali, Nigeria, Romania, and Ukraine have three. 23 countries develop two new supply deficiencies, and 50 develop one new deficiency. Different countries experience different deficiencies among different age-sex groups (Section 4.4).

Now we look at the 95% confidence intervals of the results instead of the mean (Appendix B.4). In the 2.5% scenario, southeast Asia is especially hardest hit. In the 97.5% scenario, malnourishment worsens in many countries, and most of Europe, Mexico, and Canada also develop supply insufficiencies (Figure 4.3, Figure B.4, Figure B.5). Despite the varying responses in nutritional adequacy of supply between different age-sex groups, the actual percentage decrease for the same nutrient is minimal (Table 4.1). It is interesting to note that different countries and age-sex groups experience different deficiencies, i.e. the deficiencies are not clustered (Section 4.4). Only in Indonesia and Tajikistan do all three age-sex groups experience a deficiency, but still not for the same nutrients. There are no patterns or links between deficient supplies in different age-sex groups.

To better understand the scale of the problem, it does not make sense to limit the analysis to new deficiencies, but instead to look at how many have an existing deficiency, and how that changes. At 550 ppm, men will receive enough nutrients in 27 countries, children in 18, and women in only one, i.e. only one country (Palestine) will have enough nutrient supplies for all three age-sex groups in a 550 ppm world. Women have the worst nutritional supply of the three groups due to higher iron needs from menstruation (World Health Organization and Food and Agriculture Organization of the United Nations, 2004).

The Asian and African continents experience the greatest decreases in nutritional supply, but also show the most variation in responses between countries,

while Europe and the Americas show less variation (Figure 4.5). Zinc shows the largest range in responses, while phosphorus and potassium have the smallest changes. Asia has a large diversity in the response rates, but for every element and age-sex group, the biggest decrease is always found in Asia.

4.4.3 Diet Resiliency

While high-income nations tend to fare better in terms of resiliency to nutritional supply changes, the strongest predictor of continued sufficiency is diet diversity. Diversity has the greatest protective effect on nutrient supply. Countries with the greatest drop in a certain nutrient supply are the ones with the least diverse diets (Figure 4.6). In general, countries with a cereal-centric diet fare worse than other diets, except for iron, where fruit and vegetable-centric diets fared the worst. Diets high on sweeteners also fared poorly. High consumption rates of animal products (dairy, eggs), fish, and meat conferred a protective effect against new deficiencies. While every country does experience a decrease in nutrient supply, and richer countries tend to have a smaller decrease than average, poorer countries in terms of GDP per capita do not experience a bigger decrease than average (Appendix B.2). The countries with the smallest decrease do not per se have the highest GDP per capita. For calcium, protein, and zinc, richer countries tend to be better off, but this appears to be due to high animal product consumption which is linked to increased financial status. Copper, iron, magnesium, phosphorus, and potassium show no benefit of higher GDP per capita in minimizing nutritional supply changes.

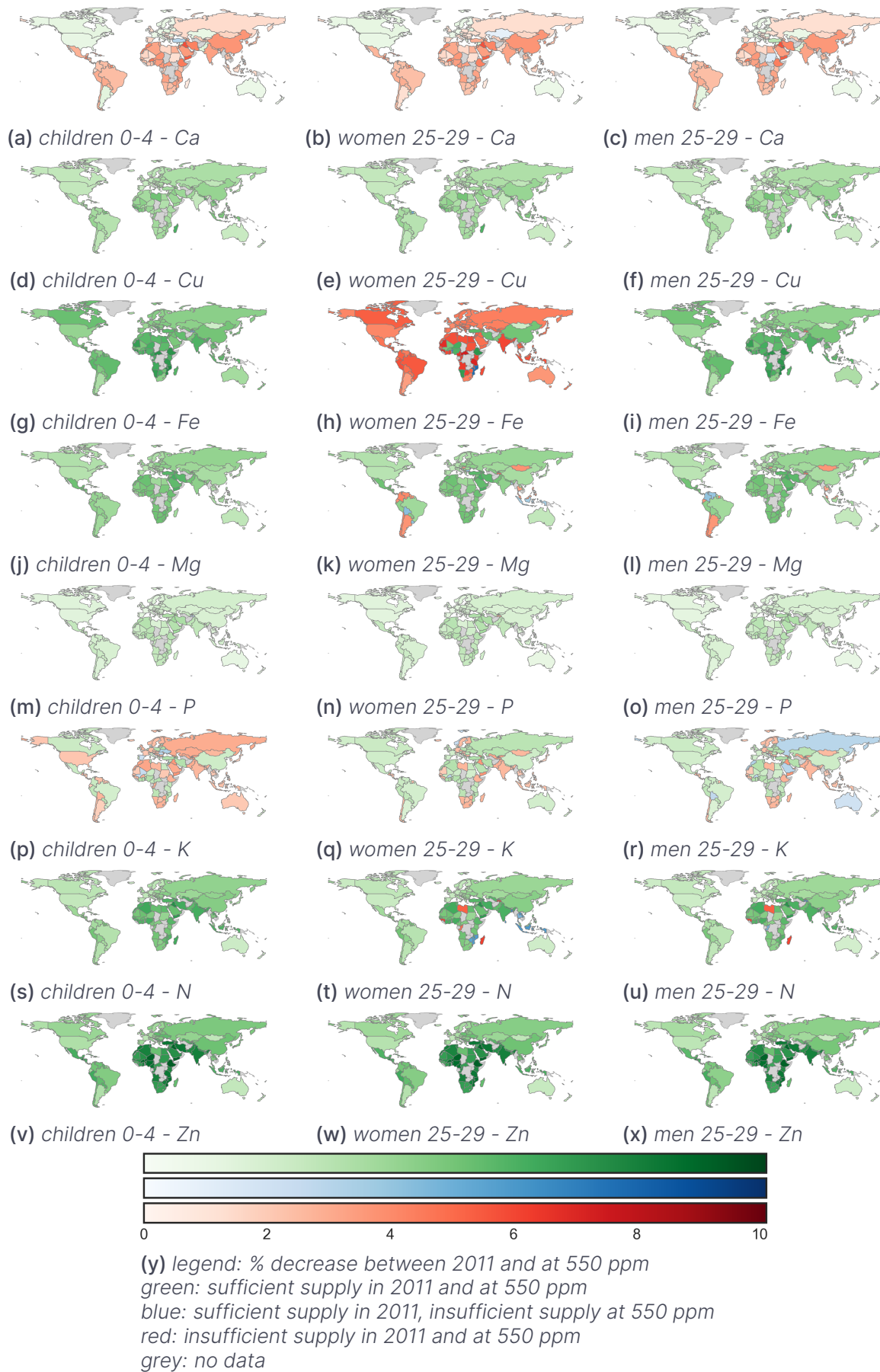
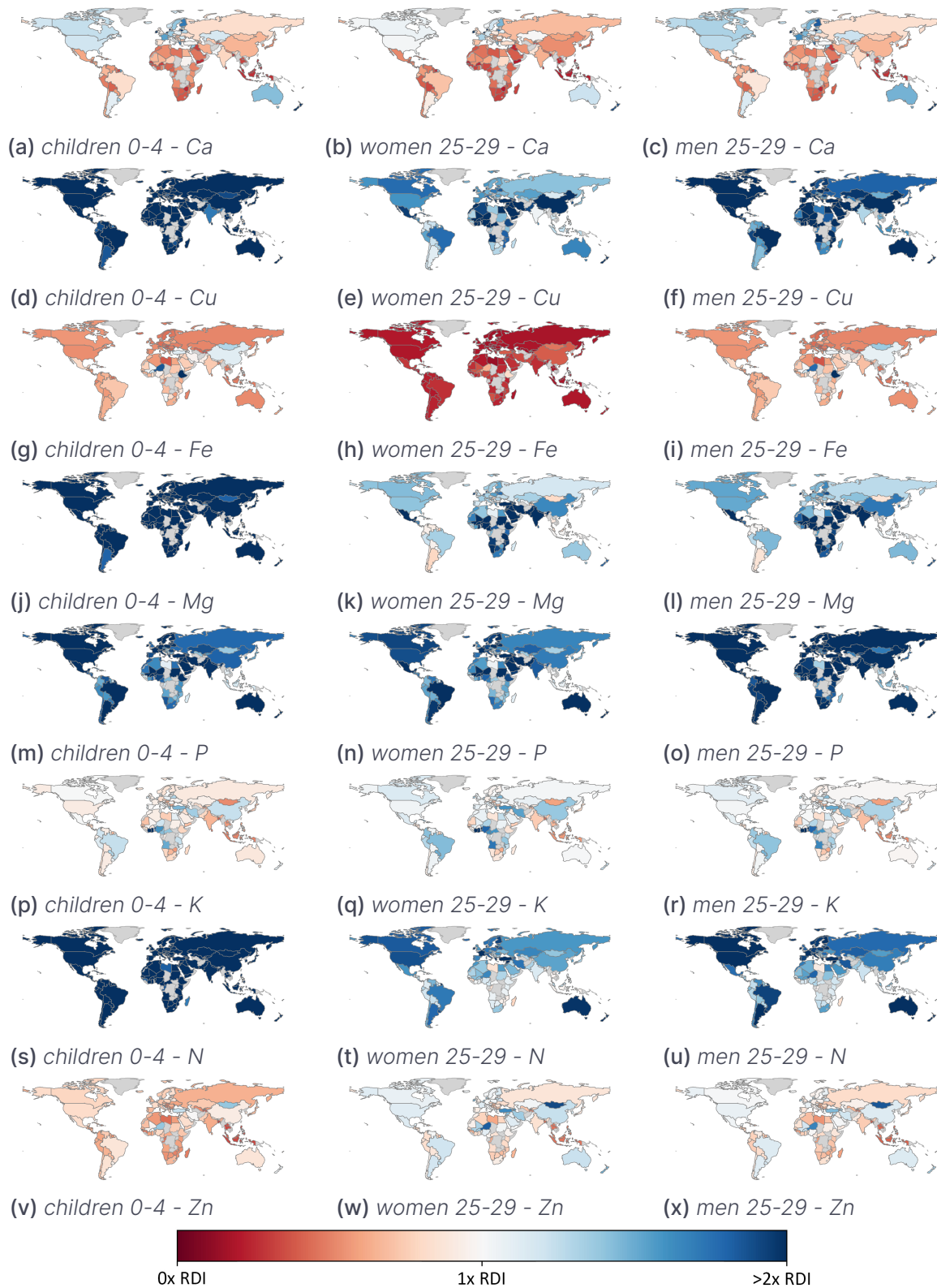


Figure 4.3: Mean changes in nutritional intake per element and age-sex group due to the direct effect on the plant ionome of an increase of CO_2 from 350 ppm to 550 ppm assuming the same dietary supply composition as in 2011. Confidence intervals shown in Appendix B.3



(y) legend: daily supplied nutrients as a ratio compared to the RDI
grey: no data

Figure 4.4: Mean daily supply of nutrients as a ratio of the RDI in a 550 ppm world assuming the same dietary supply composition as in 2011.

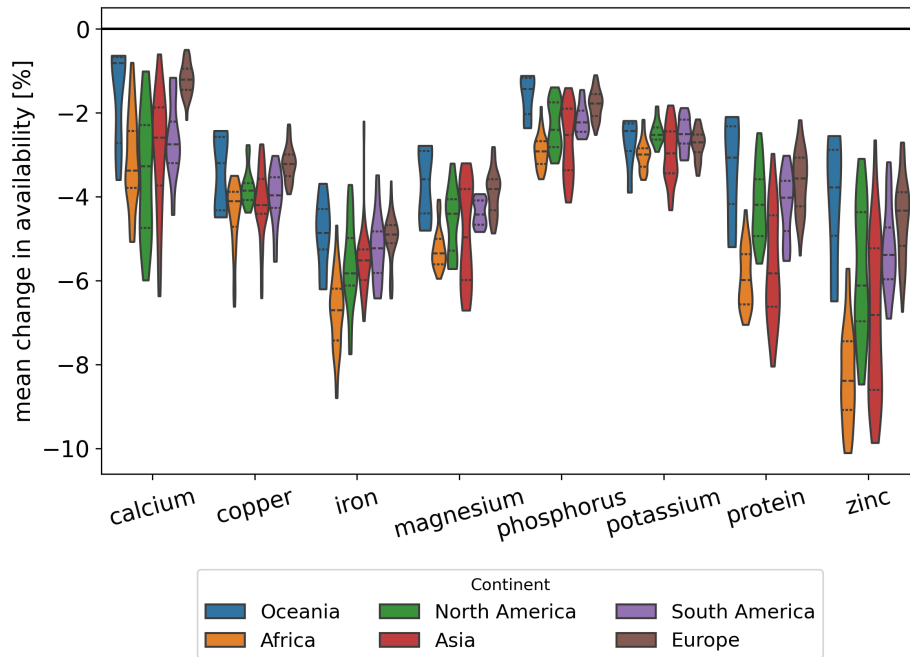


Figure 4.5: Decrease in mean percentage change to the nutritional availability by continent due to a CO₂ increase from 350 ppm and 550 ppm.

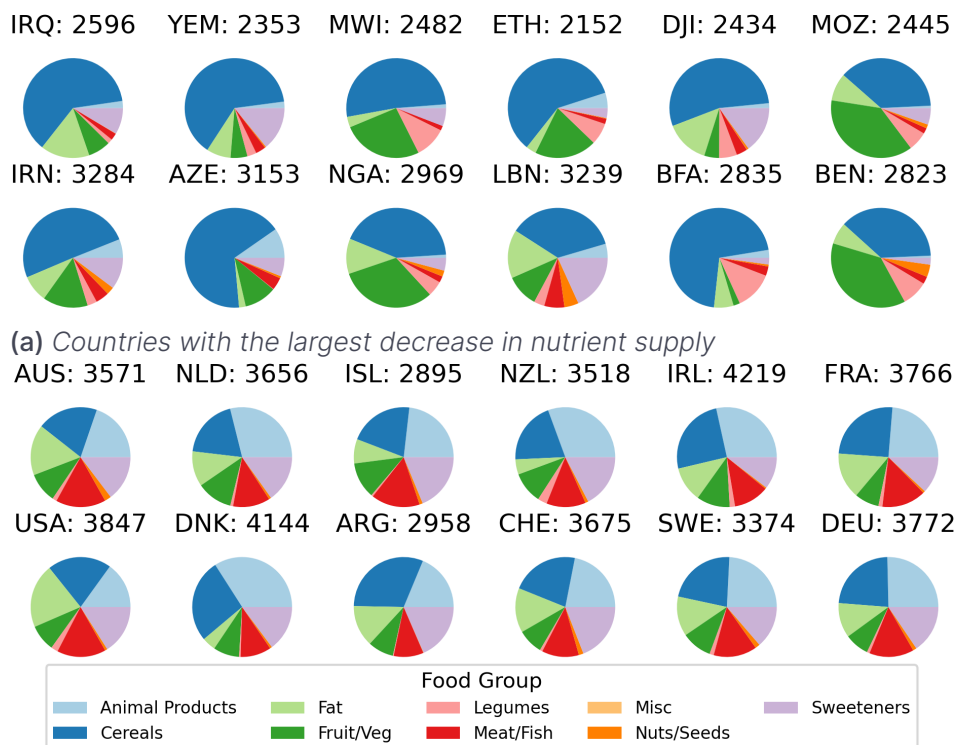


Figure 4.6: Mean consumed food per person per day for the countries with the smallest and largest changes in nutrient supply. The food distribution is given in kilocalories. The charts are shown in ascending order of the nutrient supply decrease.

4.5 Discussion

4.5.1 Limitations in Dietary Context

Globally very few countries will be able to provide their people with enough micronutrients in the future, even if they have enough macronutrients. Caloric intake was not considered, meaning that it is very possible that people can only consume enough nutrients if they (continue to) over-consume their calories. For example, only Palestine has theoretically enough nutrients for its population, but this was with a daily provision of 4,559 kilocalories for men, 3,759 kilocalories for women, and 2,256 kilocalories for young children. This is far above their daily requirement. Scaling their food intake to a macronutrient-appropriate (calorically) diet would result in an insufficient diet on a micronutrient basis. The global mean supplied kilocalories is 3,310 for men and 2,568 for women, which is sufficient on a macronutrient level but insufficient on the micronutrient level. This double burden of malnutrition - both obesity and micronutrient insufficiency - is a growing problem (FAO, 2017; Global Nutrition Report, 2021).

Even for groups where theoretically there are enough nutrients on the macro and micro nutrient scale, it is only in the context of a complete individual diet that it is possible to say if intake is sufficient. That is because nutrients can interact with each other, preventing or encouraging absorption, such as the interactions between protein, iron, and calcium. For example, a country with a protein deficiency is by default iron deficient, even if theoretically enough iron is supplied (World Health Organization and Food and Agriculture Organization of the United Nations, 2004). This should be included in future model iterations. The dietary preparation and consumption context is critical. It has been observed that dietary needs vary greatly across the world for reasons scientists do not yet understand but could be linked to interactive diet effects, sun exposure, and activity (World Health Organization and Food and Agriculture Organization of the United Nations, 2004). It is possible that certain groups have different requirements than those listed in the RDIs in Appendix B.1, either due to biological or lifestyle differences or the combined effect of diet interactions. Further, these diets were all examined without regard for any additional needs due to illness, recovery from malnourishment, or extreme levels of physical labor (Berger et al., 2022; Biesalski and Jana, 2018; Kiani et al., 2022).

4.5.2 Theoretical versus Actual Availability

This study only looks at the theoretical availability of nutrients in a country, and not how much is being consumed. This is because food waste data is notoriously unreliable. That means that this study is a best-case scenario assuming zero food waste and equal distribution of food. More realistically the food is being disproportionately delivered to - and wasted by - the wealthy, with one estimate suggesting that 1/3 of the global food production is wasted (Cederberg and Sonesson, 2011). Combining these two facts - that these diets are not being analyzed in terms of daily diet interactions and that food availability is not the same thing as food accessibility and utilization - suggests that it is likely that far

more people are being malnourished than what this study suggests.

Changes in population structure, access to food on the global markets, civil unrest, and climate change are all unpredictable and can have a negative effect on the availability of food (FAO, 2017). Changing technology can alleviate some of these challenges (Beach et al., 2019). Forecasting malnutrition status is therefore challenging. This study looks at nutritional availability assuming equal distribution of food, unchanged trade patterns, and that everything scales with the population growth. These might be a too-generous set of assumptions.

On the other hand, this study did not take into account current levels of food fortification due to a lack of data availability and time. This study focused on nutrient intake directly from food, and not from fortification or supplementation. Fortification does not always reach the most vulnerable populations (Owino et al., 2022), so this gives a better picture of realistic nutrient consumption in all groups. The primary fortified foods are salt, oil, corn, wheat, and rice flour (Owino et al., 2022). Rice, corn flour, and wheat are fortified with zinc and iron, which alleviates some of the burden (Smith, 2018b). It will be interesting to check in future research if fortification will be enough, or if additional solutions are needed.

4.5.3 Comparison with Other Models

Zinc, iron, and protein deficiencies are the main identified nutrient-related risks of rising CO₂ levels, with an estimated hundreds of millions of people expected to be placed at risk of a deficiency and a worsening of deficiency in the two billion people already suffering from it. Countries already struggling the most with malnutrition will be disproportionately affected (Myers et al., 2015, 2017; Medek et al., 2017; Smith et al., 2017; Smith and Myers, 2018; Weyant et al., 2018; Beach et al., 2019). Loladze (2014a, p. 21) explicitly warns, "As tempting as it can be to partition the current dataset into many categories and cases (e.g., Zn in fruits, Fe in tuber, Cu in annuals, multiple CO₂ levels), only by fragmenting the data into sufficiently large categories an adequate statistical power can be retained". The model from Chapter 3 is sufficient, but ideally everything should have been included as factors for finer control of the CO₂ effect on different crops. Other models of health impacts all split the data (e.g. Myers et al., 2015; Smith et al., 2017; Myers et al., 2017; Beach et al., 2019; Weyant et al., 2018). These extensions all base their works off of Myers et al. (2014) which has a very small sample size and is limited to six crops. The only exception is Beach et al. (2019), which uses both Myers et al. (2014) and Loladze (2014b). They all suffer from the same issue of losing power from overpartitioning their data, pulling data from an inconsistent population, and having insufficient sample sizes. They also use 550 ppm as the average elevated CO₂ level, which is close to the mean used by Myers et al. (2014) in the original experiments, but not in the extended experiments they are referencing. These errors have been fixed in our model. Despite the methodological differences, it is interesting to compare the results between these studies.

Myers et al. (2015) uses different divisions between world regions, so we can only compare our calculated zinc intake for India, China, and the global average.

Our results are a higher intake in India and China, but a lower global average than what they calculate. These differences are only a few percent off from each other. Weyant et al. (2018) calculated the effects of iron and zinc decrease in terms of disability-adjusted-life-years which makes it difficult to directly compare the results, but we both reached a similar conclusion that iron and zinc decreases disproportionately affect southeast Asia and sub-Saharan Africa. Medek et al. (2017) estimated protein deficiencies in 2050, and their confidence intervals are much wider, and always overlap with ours for the decrease in certain crops. Our calculated global decreases in protein and which countries are hardest hit are similar. Compared to Smith et al. (2017), our calculated change in iron is slightly higher (about 3% stronger). This is because we have more data and differentiation between different crops. Beach et al. (2019) examined zinc, iron, and protein using both the Myers et al. and Loladze datasets. Their results are lower than our calculated results, with zinc being a third of the decrease and iron only half of our calculated decrease. Beach et al combined different experiment types and added in a skew-normal response to the data, which could account for this difference, on top of having significantly less data and fewer differentiation between crop types. The response rate trends do appear similar. Overall, the papers show similar results, suggesting confidence in the appropriateness of our methods. Our model benefits from a larger dataset, and is thus able to differentiate the response rates of crops. Further research on country specific cultivars for staple crops and on underrepresented foods such as non-C3 plants, nuts, seeds, cruciferous vegetables, fruits, and spices would benefit the model accuracy and better capture the effects.

4.5.4 Gender Inequality and Nutrient Deficiencies

Gender inequality will worsen due to CO₂ rise-induced malnutrition. Women experience the most severe and numerous food supply deficiencies of the three examined age-sex groups both before and after accounting for the changing plant ionome (Section 4.4). While it appears that men develop more deficiencies than women or children, this is only because women are already deficient (Section 4.4). Deficiencies in women are primarily due to their increased iron needs because of their menstrual cycles (World Health Organization and Food and Agriculture Organization of the United Nations, 2004). Globally a third of women are anemic, contributing 20-40% of maternal deaths, stunted development, and a 4% reduction in GDP (Hélène Botreau and Marc J. Cohen, 2019). Looking at the amount of food theoretically available to each age-sex group, men have on average 1.23 times more food than women, although their RDIs are equal for calcium, copper, and phosphorus and women need 2.15 times as much iron as men. This food distribution is only appropriate for magnesium, potassium, and protein, and is inappropriate for zinc in men as they need 1.4 times as much (Appendix B.1). In other words, food supply and distribution are not appropriate for each sex's specific needs (Figure 4.4). This imbalance worsens during pregnancy when a woman's nutritional needs increase dramatically (World Health Organization and Food and Agriculture Organization of the United Nations, 2004). This fact is not

captured yet by the results. This result is similar to published findings, where women are more likely than men to be food insecure in every region of the world (FAO, 2017).

Women bear the brunt of nutritional deficiencies and these deficiencies will worsen due to CO₂ rise. This fact should play a role in discussions about gender equality and access to food. Women are more food insecure due to increased vulnerability to food availability, access, utilization, and stability. Additionally, women are tasked with solving hunger within their families and are unusually the ones that 'eat least, last and least well', shifting their diets to cheaper and less diverse diets that lack key nutrients from pregnant women and young children (Hélène Botreau and Marc J. Cohen, 2019, p. 43). Food availability is thus mostly adapted to the needs of men, and not the unique nutritional needs of growing children and fertile women. There is a difference between a country that technically has enough food for everyone and a country that provides enough food for each resident, and care should be taken that nutrients are distributed equally on the basis of need to all age-sex groups.

4.5.5 Economic Aspects, Food Culture, and Diet Diversity

Diet diversity is a greater indicator for continued nutritional sufficiency than high-income (Appendix B.2 and Figure 4.6). For calcium, protein, and zinc, high-income nations are more resilient to nutritional supply changes, but this is a result of their increased diet diversity and increased animal product consumption which is linked to their financial status (Finley et al., 2017). Animal products are more nutrient-dense than plant foods, making it easier to achieve nutritional sufficiency in a limited dietary context. In this study, it is presumed that animal products do not change in nutritional composition. This is a limitation of the study design due to insufficient research, suggesting again that our results are a conservative estimate. This research gap has been highlighted by other meta-analyses who were forced to make the same assumption (Myers et al., 2015).

Countries with the smallest decrease do not per se have the highest GDP per capita. Copper, iron, magnesium, phosphorus, and potassium show no benefit of higher GDP per capita in minimizing nutritional supply changes. Countries with a staple crop are primarily found in Asia and Africa, which shows the largest decrease in mean nutrient availability. Countries with no staple crop, such as much of North and South America, show much more tempered responses. While complicating a fortification plan, a diverse diet is more robust towards climate impacts (Figure 4.6). This trend is visible across the elements. The biggest loss of calcium, copper, and iron is in Asia, driven by the loss from cereals and rice. This is due to a grain-heavy diet in these countries. Countries that eat significant amounts of legumes, such as Madagascar and South East Asia even increase their copper levels at the 97.5% confidence interval. Other European and American countries only experience a marginal decline. Magnesium, phosphorus, potassium, and protein losses are twice as high as the global average in the Middle East, from their cereal consumption. Zinc losses are up to four times as high from cereal in the Middle East, and two times as high in south and southeast

Asia due to their cereal and rice consumption respectively. Countries with the greatest losses are consistently the ones with the least diverse diets, which also are typically grain-centric diets.

4.5.6 Possible Solutions

All countries in the future, except Palestine, will need to change their food availability and composition to allow all their residents to consume enough nutrients. Biofortification, food fortification, and supplementation are effective (Stevens et al., 2022) and a possible solution, depending on local social acceptability (Zhu et al., 2018; Owino et al., 2022). If a country is dependent on a staple crop, such as rice in much of Asia where people are dependent on it for over half of their daily calories, then genetic modification or switching cultivars could be a way to bolster nutrient supply without requiring behavioral change (UNSCN NEWS, 2017). For countries with no staple crop, or where supplementation or (bio-)fortification is not an option, social change towards different dietary patterns is needed and government-recommended diets may need to change to accommodate that (Owino et al., 2022).

4.6 Conclusion

Malnutrition is already a global problem, and CO₂ rise will both directly and indirectly worsen this. Countries will be unable to provide enough nutrients (calcium, copper, iron, magnesium, phosphorus, potassium, protein, zinc) from food solely due to changes in the plant ionome, worsening the hidden hunger problem, with about half of the world developing new deficiencies. We are looking at an incoming growing mass malnutrition event so we need to change how we think about and consume food. It is not safe to assume that sufficient caloric intake will imply a sufficient micronutrient intake, and the gap between the two will only continue to widen. A healthy diet composition is a concept that will need to adapt to climate change. We are already near the halfway point between this study's baseline (350 ppm) and future forecasts (550 ppm). Malnutrition is not just a problem of poverty. Climate change is not a future far-away problem of worsening tropical storms and melting ice caps. Everyone will be affected by climate change-induced malnutrition. The problem is already here, and it is on our dinner plates.

There is global inequality, and unfortunately, the changing plant ionome will exacerbate this, although not one country will be spared the effects of CO₂ rise on their nutritional supplies. All continents but North America will experience changes in the theoretical availability of nutrients in a 550 ppm world. Taking into account which countries already have deficiencies, every country in the world has a supply deficiency except for Palestine. Asian countries followed by African countries have the largest percentage of nutrient decrease, although there is considerable variation throughout the continent. Europe has both the smallest decrease and the smallest variation, similar to North America. Protein,

zinc, and iron are the hardest hit nutrients and are already critical nutrients on the edge of malnourishment in many populations. Phosphorus and potassium deficiencies will increase as well. New deficiencies are not clustered by country or age-sex group, owing to their different intakes and needs. Young men have the least impact, followed by children, while young women are hit hardest, driven primarily by iron needs. This stratified impact based on age and gender is worth further examination and adds another dimension to the global inequality aspect of climate change. Women are more vulnerable to climate change-induced malnutrition and often receive a less nutritious portion of food than other age-sex groups. This model is conservative, neglecting changes to animal products, diet interactions, food waste, and food availability and distribution. If food intake is adjusted for waste, are people still eating enough micronutrients, let alone in the future? Future iterations of this research would benefit from adding in waste models, using more recent trade data, accounting for the dietary composition and nutrient interactions, and updating food nutritional content information. The calculated effects are unlikely to be evenly applied, so vulnerable populations such as women and the poor will most likely have much more severe nutrient deficiencies than what is calculated here. (Bio)-fortification and supplementation can alleviate some of these burdens, but the appropriate solution will not be found until the actual effects can be modeled or measured. More research is needed on the changing plant ionome and actual food consumption. Even at a conservative level, the global average decrease in nutrients ranges between 2.33% to 6.37% depending on the nutrient analyzed. The decrease in food nutrient density is worrisome and significant; it will worsen the hidden hunger problem of the double burden of malnourishment and obesity.

Despite the differing national diets, one trend remained consistent: diverse diets are more robust to impacts from the changing plant ionome. Grain-centric diets tended to fare the worst, followed by sweetener-heavy diets. Animal product-heavy diets fared the best. However, this could be because the research design assumes no change for animal products, and not due to a protective effect from the nutrient density of animal products. When compared to GDP per capita, rich countries with high animal product consumption have the least impact, but poor countries are not necessarily impacted more. Dietary diversity, not GDP, determines the robustness of a diet against rising CO₂ levels.

5. Future Research Directions

The two subquestions did answer the main research question but also highlighted each other's inadequacies. The effect of the changing ionome on nutritional supply is great, despite the conservative method used to calculate this. This brings up already two critical research avenues: 1) increase the accuracy of the plant ionome model, and 2) decrease the conservativeness of the model by improving data on actual consumed food.

5.1 Increase Accuracy of Nutritional Changes

5.1.1 Focus on Foods Other Than C3 Grains and Soybeans

While it is understandable that the majority of research focuses on staple C3 crops (rice, wheat, soybeans), the sparse research on non-C3 plants and non-grain edible plants as well as on non-plants means that changes in critical nutrients from other foods are not well-observed. More data is needed to refine the confidence intervals, analyze different food groups including the underrepresented C4 group and unrepresented CAM group, as well as collect more data on a wider range of nutrients. Research focuses on the world's most commonly eaten crops - rice, wheat, and soy - but selects cultivars most relevant to their region, and this creates a bias. Other works, and data exploration that has been excluded in this analysis, show considerable variation between cultivars (Myers et al., 2014). Many countries lack databases on the nutritional composition of locally eaten food, making it harder to choose appropriate crops to study for the changing ionome, and in turn, to see how their supplied nutrients will change. Selecting crops that are financially significant or commonly eaten globally neglects to study crops that offer critical micronutrients such as selenium in nuts. There is a research gap on how this will affect animal products and the fungi kingdom, which now provide a significant amount of nutrients.

5.1.2 Reassess RDIs in the Context of Changing Micronutrients

It is easy to conclude that because rice and wheat have the biggest impacts, they should be studied more, but it may be because they are so well-studied, that the large impacts are known. Similarly, as a common deficiency, many studies focus on iron and zinc. This focus on critical minerals seems logical, but the

reverse is equally important: minerals that are critical because they are harmful to human health are barely studied, while preliminary results show that they may be increasing. This is a big blind spot. Similarly, RDIs don't cover trace nutrients because it's assumed that these needs are met if other micronutrient needs are met (The United Nations University, 1982). But will this assumption hold if they are also affected by the changing ionome? Trace minerals and their place in RDIs deserve renewed attention.

5.1.3 Understanding Longterm Effects

Multi-generation experiments are also needed - multi-generation experiments are not included in this database and are too few to be used in their database. Once we understand what the effects of increased CO₂ are on plants, we need to move on to a better understanding of the long-term effects. There is evidence to suggest that this will be different than the single generation changes (Lemon, 1983; Li et al., 2019).

5.2 Increase Model Realism

5.2.1 Update GENUS Model

GENUS uses trade data from 2011, which could be improved with more recent data that reflects changing dietary patterns. Including information on population demographics and analyzing more age-sex groups would be more insightful on the differential impacts on global inequality as well as show how this can change as the population composition shifts. Will nutrients become more or less available to vulnerable groups? Additionally, there is a mismatch in the calculated nutritional content and that provided by alternative GENUS datasets, so a clearer model of food nutritional content would help realign these datasets. Nutritional information of locally consumed foods would improve the accuracy.

5.2.2 Look at Consumed Instead of Supplied Food

The results are a conservative estimate of the true effect because the model uses the total amount of food supplied in a country, not the amount consumed. This has two implications: 1) critical crops may be wrongly identified, and 2) the overall impact, especially on vulnerable populations, is not fully captured. Even without accounting for food waste, many countries have a supply deficiency. How much more severe the actual consumed deficiencies are is difficult to say. It is not realistic to scale the food intake to a certain caloric amount because different foods are likely to be wasted at different rates. Using the calculated percentage decreases to determine priority crops or nutrients for research could have misleading results if 'priority crops' are disproportionately wasted. The overall impact is also underestimated. If food intake is adjusted for waste, are people still eating enough micronutrients, let alone in the future?

5.2.3 Model Actual Eating Patterns

True nutritional availability in the context of a complete diet is currently missing. True deficiencies should be better modeled as the model did not account for the interactive effects of nutrients or preparation methods. For example, a protein deficiency results in an iron deficiency, regardless of intake. Other nutrients, such as calcium and protein antagonize each other. These interactions are currently not included, meaning that the true amount of deficiencies is higher than presented.

Future dietary patterns, such as the predicted increase in highly processed foods, refined oils, and animal products, will play an interesting role in nutritional availability. Will this be a boon or aggravate the effects? This study also only focused on minimally processed food, but especially in the West people are eating more processed foods than unprocessed foods (Beal and Ortenzi, 2022). The nutritional absorption will likely differ, and how will this changing dietary pattern affect the nutritional intake? Are processed foods more or less bioavailable, and in what contexts? Similarly, what will be the effect of a shift in the West towards more plant-forward diets and in developing countries to eating more animal products?

5.2.4 Providing Realistic Solutions

Is it physically possible to eat enough food to accommodate for these losses without dangerously overconsuming other nutrients, and what impact does that have on the macronutrient diet composition? Are dietary adjustments sufficient to solve any potential inadequacies, and if so, how should governmental dietary recommendations change? Alternatively, can these losses be mitigated through switching to a different cultivar, or through genetic modification and bio-fortification? Is post-processing fortification a better option for certain countries? What is the social acceptance for any of these options? And what are bottom-up solutions that be implemented, such as community-led nutritional education?

5.2.5 Synergize with Government Recommended Diets

Previous research on the environmental and health impacts of different diets has shown that following government-recommended diets is a win-win (Behrens et al., 2017), but will these guidelines be appropriate in the future for sufficient nutrient intake? Re-evaluating them under the context of changing nutritional values could be an opportunity for countries to promote a diet better for human and environmental health. Only 94 countries have a recommended diet. Government dietary guidelines are useful to "inform coherent actions across food systems, covering actors and institutions from production to consumption" (Wijesinha-Bettoni et al., 2021). This forecasting model of nutritional intake can be useful in helping countries draft a climate change-adapted dietary guideline, and help countries with existing plans to update it appropriately while centralizing sustainability in their food system.

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A . Appendix: Altered Ionomes

A.1 Changes to the Loladze (2014) dataset

Table A.1: Changes made to the original Loladze (2014a) dataset.

Paper	Change
Erbs et al. (2010)	added in N50/N100 and year Fixed iron and zinc calculations for Barley added in Crude Protein Concentration (CP) as a proxy for Nitrogen for both grains fixed year added in cultivar name
Fernando et al. (2012)	added in values for N, Mg, Na, Fe, Ca, S, P, Zn, K, Cu, Mn
Fernando et al. (2014)	added in values for N
Högy and Fangmeier (2009)	one B value is actually of Al added in N
Högy et al. (2009)	added in protein from figure 5
Högy et al. (2010)	fixed Ni (forgotten + sign) added in protein added in missing 'n' for N
Högy et al. (2013)	one B value is actually of Al and added in N
Khan et al. (2013)	fixed Zn (Astra and Eureka cultivars were switched) was originally listed as Kan 2012 fixed scientific name to <i>Solanum lycopersicum</i> (formerly thought to be different plants, but are the same)

Continued on next page

Table A.1: Changes made to the original Loladze (2014a) dataset. (Continued)

Paper	Change
Manderscheid et al. (1995)	fixed some values using adjusted means (Loladze's method was unclear)
Wroblewitz et al. (2013)	fixed sodium for N50 2002, minute change to Zn N50 2000 added in N (CP) for both
Yang et al. (2007)	fixed minor errors, added in N
Guo et al. (2011)	was originally listed as Guo 2013 updated cultivar name to include number
Pérez-López et al. (2014)	was originally listed as Pérez-López et al (2013)
Chagvardieff et al. (1994)	fixed Ca values listed results as edible
Baslam et al. (2012)	listed as edible
McKeehen et al. (1996)	listed as edible changed radish foliage to root
Barnes and Pfirrmann (1992)	added in edible portion of radish added in elevated ozone measurements
Yamakawa et al. (2004)	changed from 'F' to 'E'
Jain et al. (2017)	changed from 'F' to 'E' added cultivar name
Prior et al. (2008)	added in the edible portion from the article updated cultivar names
Fernando et al. (2012)	updated number of replicates updated delta and ln added in extra N entries
Fernando et al. (2014)	updated numbers
Fernando et al. (2012b)	redid all calculations - previous methods were unclear
Heagle et al. (2003)	fixed Zn for 80 O3, N for 45 O3 in Superior cultivar added in 540/370 dataset
Fangmeier et al. (1997)	added in the nitrogen fertilizer (NF) results for NF and NF+
Pleijel and Danielsson (2009)	added in intermediate result for 1995
Pang et al. (2005)	added cultivar name

A.2 Changes to the Dietterich (2015) dataset

- Changed Bekoaba 'Ca' (2010, 160) to 0.625 assuming $<0.01=0.005$
- Changed Akitakomachi 'Ca' (2010, 80) to 1.9 assuming $<0.01=0.005$
- Fixed missing B by setting <1 to 0 in CSV file
- Updated cultivar names, e.g. Glycine max 'Williams' changed to 'Williams 82', 'SY63' to 'Shan You 63'

A.3 (Meta-)data in the combined database

Table A.2: (Meta-)data stored for each entry in the combined database

(Meta-)Data	Description
naming	full scientific name Genus, Species, Cultivar, and common name
classification	C3/C4, tissue, and study type
study conditions	aCO ₂ and eCO ₂ level added CO ₂ additional information
cofactors	elevated temperature irrigation sowing time phosphorous, nitrogen, and ozone application
experimental details	year (for multi-year experiments) latitude and longitude* country* <i>*for FACE/OTC experiments only</i>
bibliographic	reference origin (from Loladze, Myers, Dietterich, or Snowball) year published
results	# of replicates element delta ($E - A$)/ A natural log of the response rate $\ln(E/A)$

A.4 Publication Bias

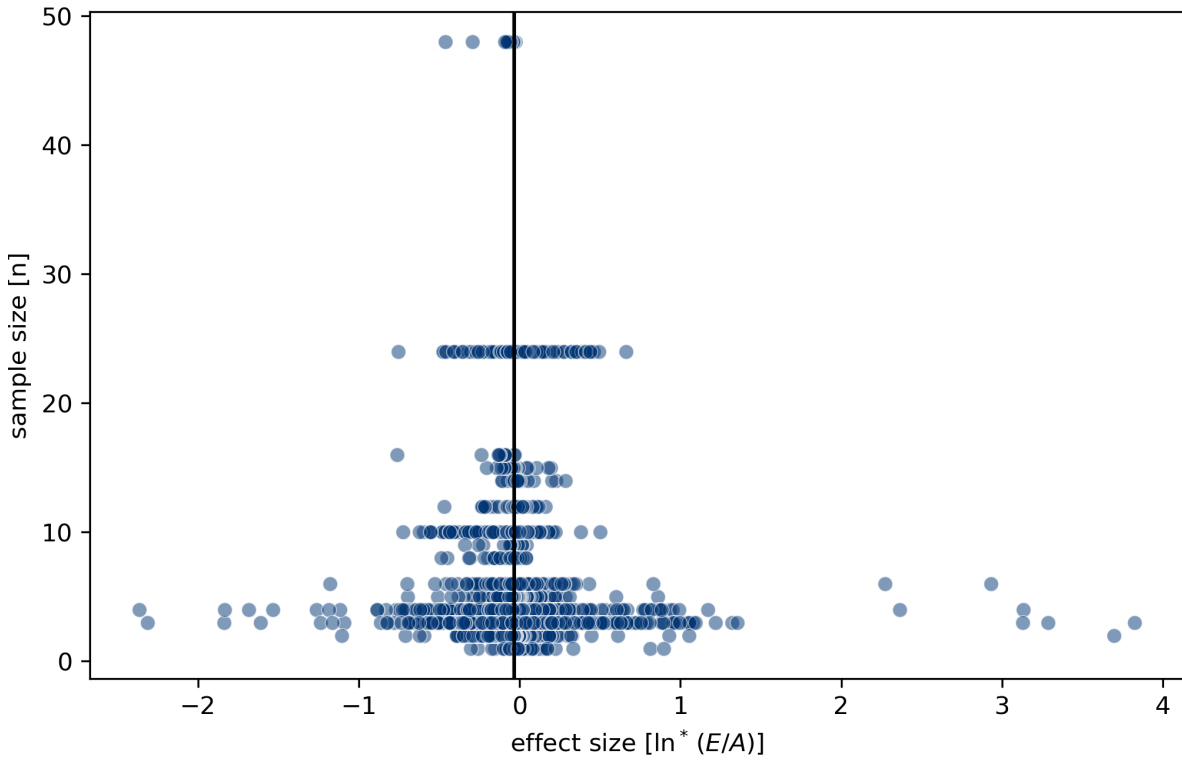


Figure A.1: Publication bias of the whole adjusted dataset. A funnel plot tests for publication bias in the whole dataset. The black line is the mean effect of the population. The term 'adjusted $\ln(E/A)$ ' is equivalent to ' $\ln(G/A^*)$ ' and refers to the standardized natural logarithm of the response at the standardized adjusted elevated CO_2 levels divided by the response at standardized adjusted baseline ambient CO_2 levels.

A.5 Outliers by Different Cut-off Criteria

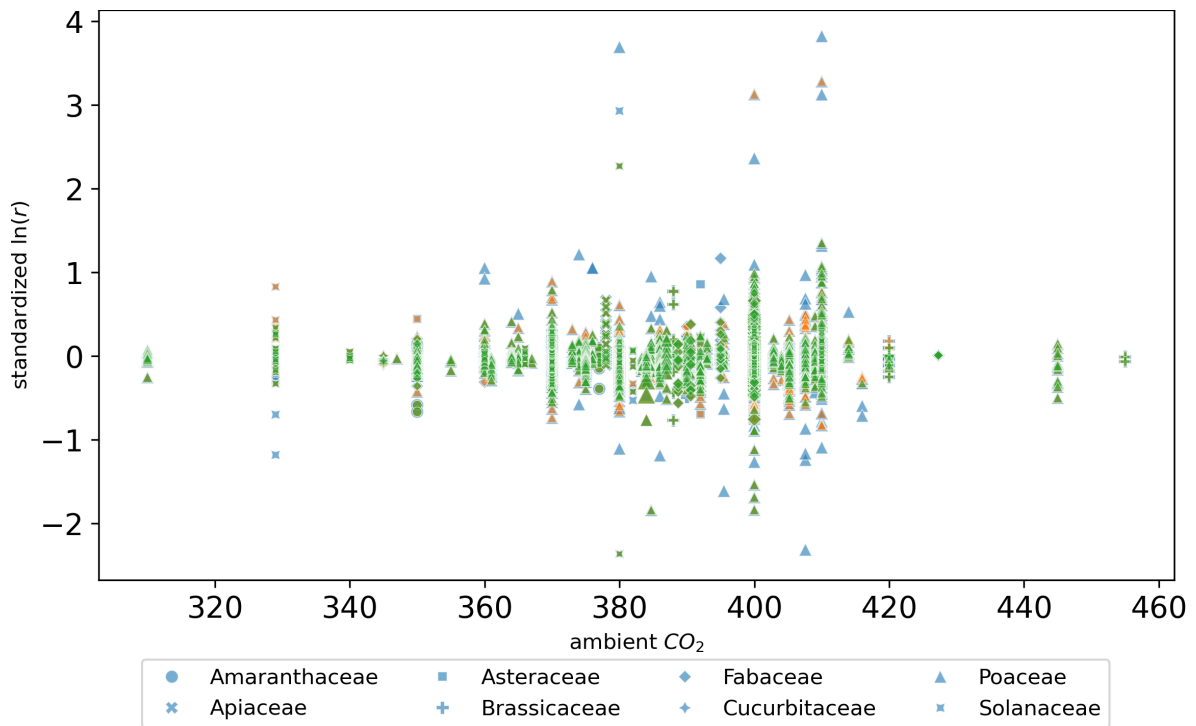


Figure A.2: Outliers as detected by different IQR cutoffs. Outliers in the dataset (blue) detected by the IQR method using 1.5 IQR (green) and 3 IQR (orange) cut offs. Outliers are detected relative to other datapoints in the same Genus of the same tissue type and element.

A.6 Bootstrapping Results Comparing Indoor and Outdoor Experiments by Photosynthetic Pathway

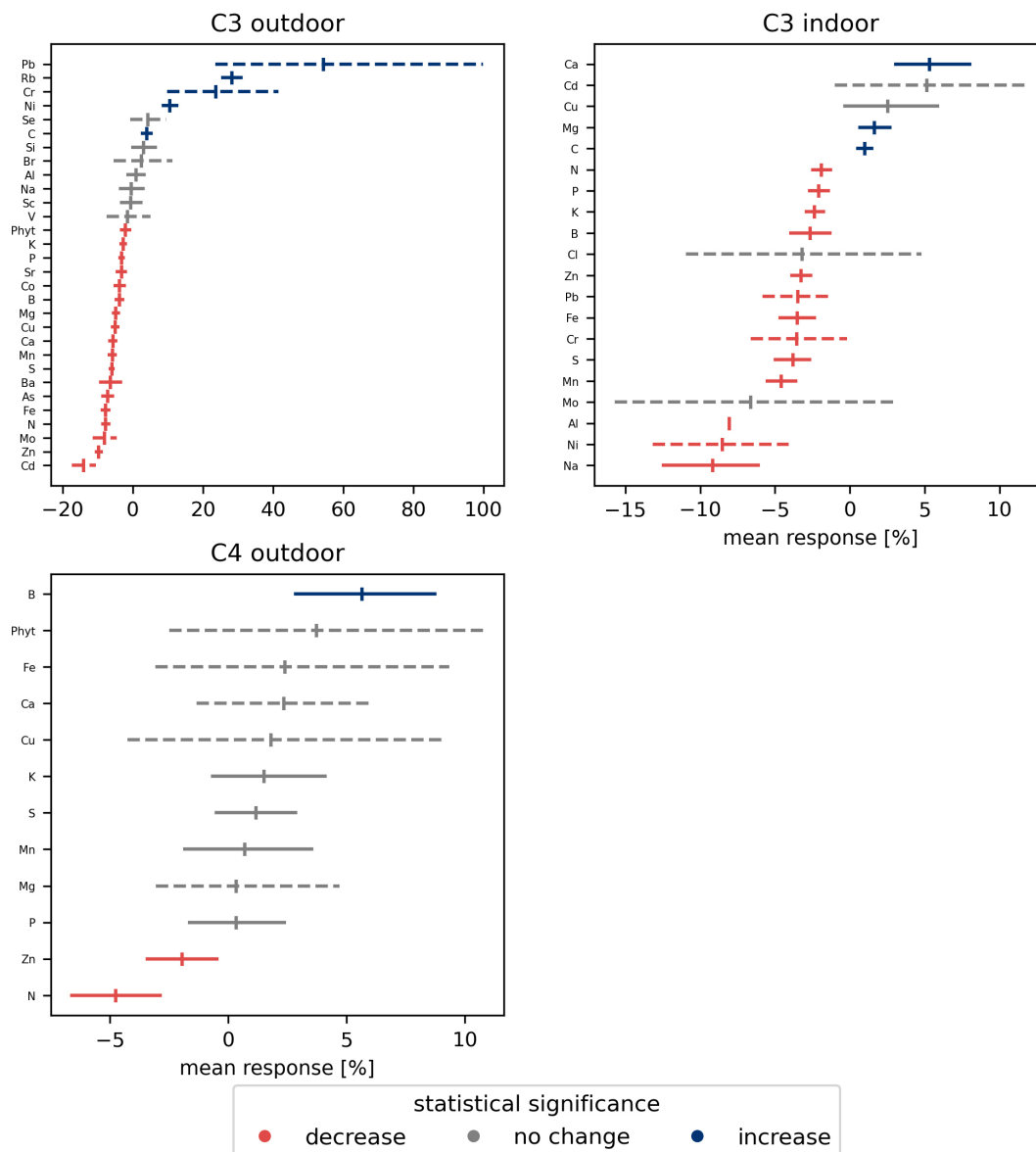


Figure A.3: Bootstrapped percentage change per element, sorted by photosynthetic pathway and experiment type.

Values are given as percentage change for the dataset split by different drivers, given by the mean (tick) and 95% confidence interval (line) of the 10,000 bootstraps. Only results with power > 0.8 are shown and are color-coded by their statistical significance at $\alpha = 0.05$. BG stands for 'below ground' and includes roots and tubers. Reproductive contains all fruits, seeds, grains, and pods. Rice grains are listed separately due to their unique growing conditions.

A.7 Bootstrapping Results for Indoor Experiments

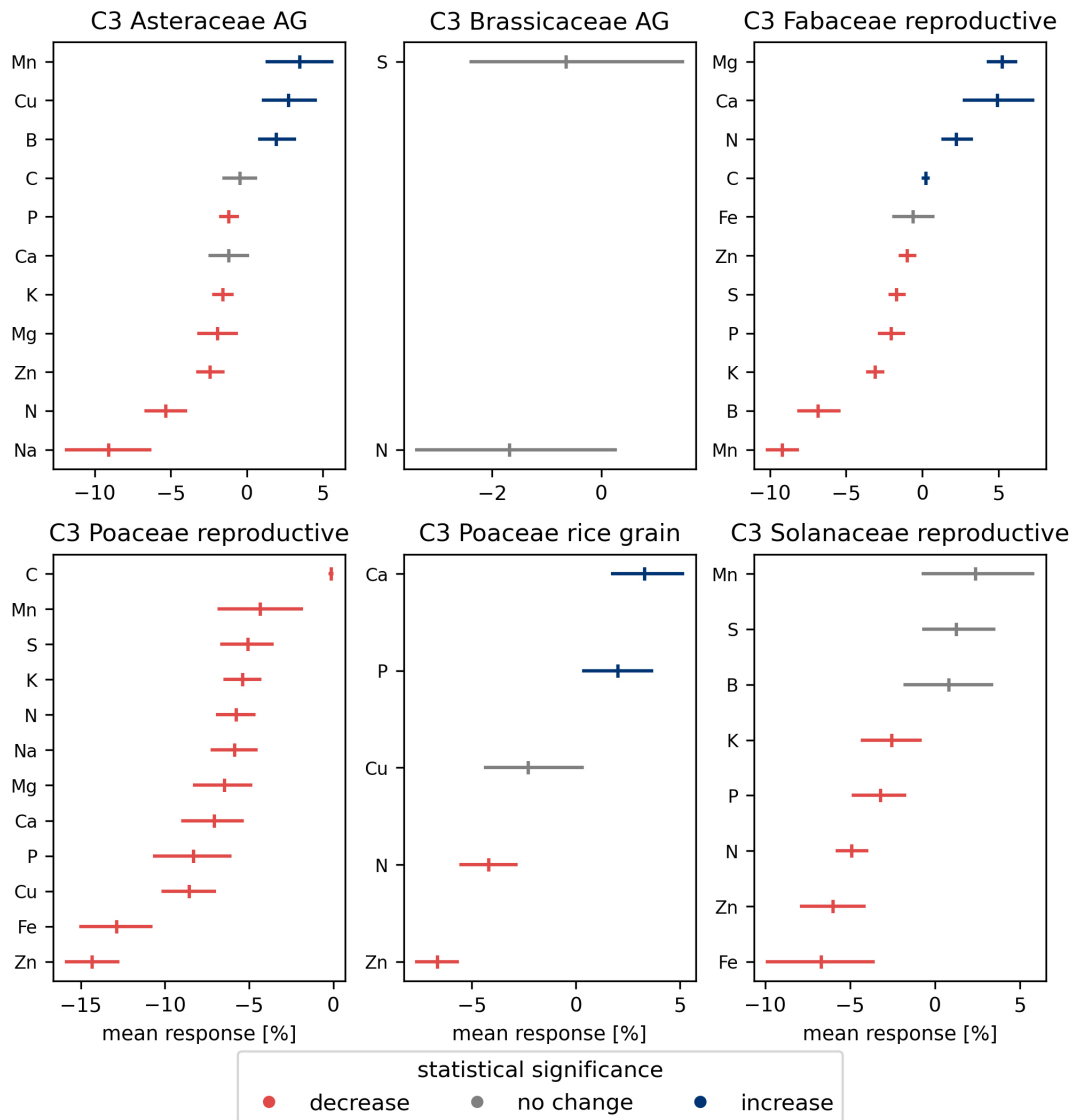


Figure A.4: Bootstrapping results split by combined main drivers.

Results shown as percentage change per element, sorted by photosynthetic pathway, family, and tissue type. Values are given as percentage change for the dataset split by different drivers, given by the mean (tick) and 95% confidence interval (line) of the 10,000 bootstraps. Only results with power > 0.8 are shown and are color-coded by their statistical significance at $\alpha = 0.05$. BG stands for 'below ground' and includes roots and tubers. Reproductive contains all fruits, seeds, grains, and pods. Rice grains are listed separately due to their unique growing conditions.

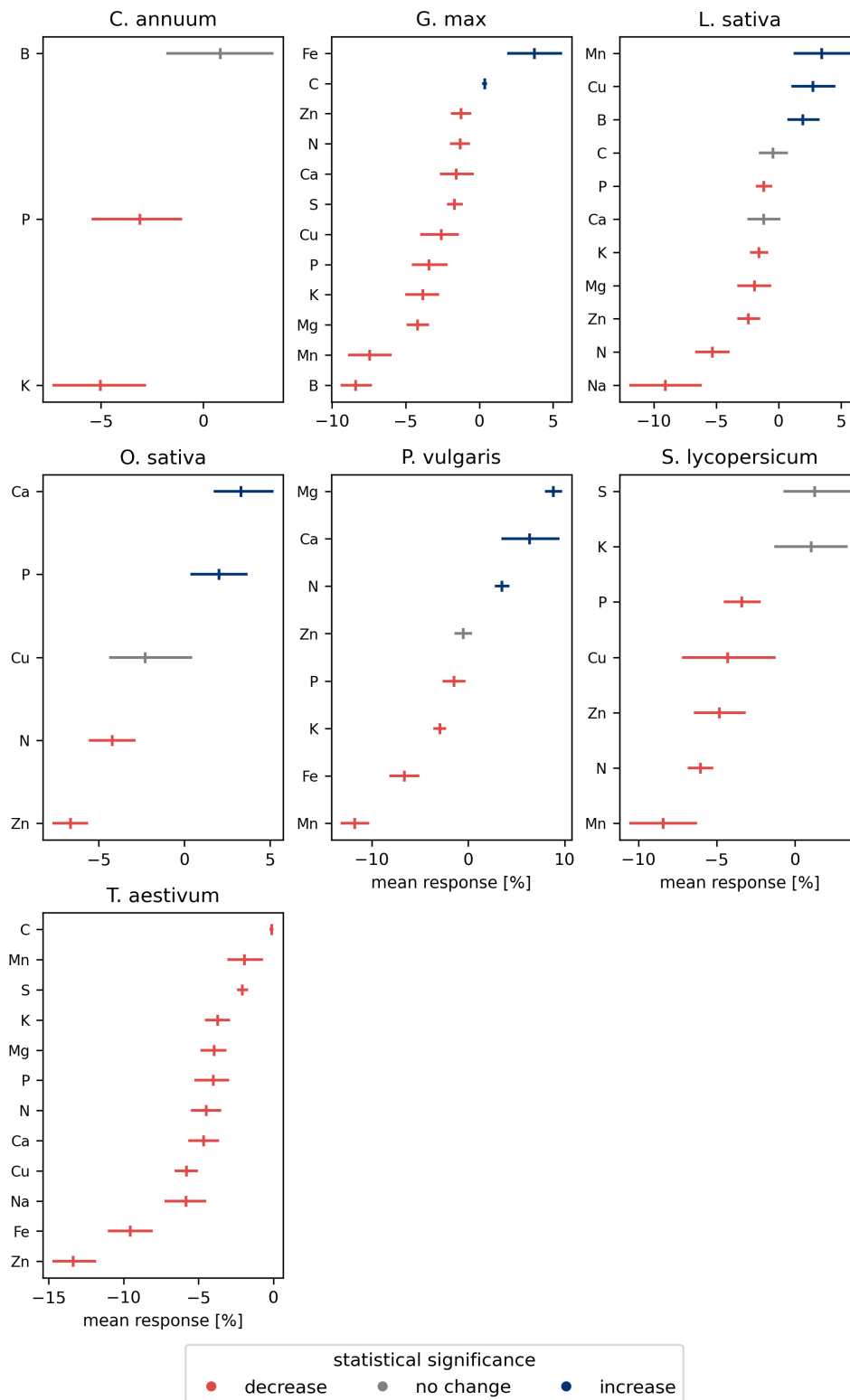


Figure A.5: Bootstrapping results split by main drivers combined for important species. The percentage change per element, sorted by photosynthetic pathway, family, and tissue type. Values are given as percentage change for the dataset split by different drivers, given by the mean (tick) and 95% confidence interval (line) of the 10,000 bootstraps. Only results with power > 0.8 are shown and are color-coded by their statistical significance at $\alpha = 0.05$. All species are C3 plants with the exception of C4 plant *S. bicolor*.

B . Appendix: Nutrition

B.1 Recommended Daily Intakes (RDIs)

Table B.1: Governmental Recommended Daily Intakes for selected nutrients. Nutrients separated by a slash denote 'breastfed/other'.

	Unit	Bioavailability	0-6m	7-12m	1-3y	4-6y	F 25-29	M 25-29	Reference
Ca	mg		300/400	400	500	600	1000	1000	WHO & FAO (2004)
Cu	µg		200	220	340	440	900	900	NIH 2022a
Fe	mg	15%		6.2	3.9	4.2	19.6	9.1	WHO & FAO (2004)
		12%		7.7	4.8	5.3	24.5	11.4	
		10%		9.3	5.8	6.3	29.4	13.7	
		5%		18.6	11.6	12.6	58.8	27.4	
Mg	mg		26/36	54	60	76	220	260	WHO & FAO (2004)
P	mg		100	275	460	500	700	700	NIH 2023
K	mg		400	860	2000	2300	2600	3400	NIH 2022b
Zn	mg	high	1.1	0.8/2.5	2.4	2.9	3.0	4.2	WHO & FAO (2004)
		moderate	2.8	4.1	4.1	4.8	4.9	7	
		low	6.6	8.4	8.3	9.6	9.8	14	

	Unit	0-1m	1-2m	2-4m	4-12m	1-4y	4-7y	F 25-29	M 25-29	Reference
N	g	8	8	8	11	14	18	48	57	Richter et al. (2019)

B.2 GDP per capita versus nutrient decrease

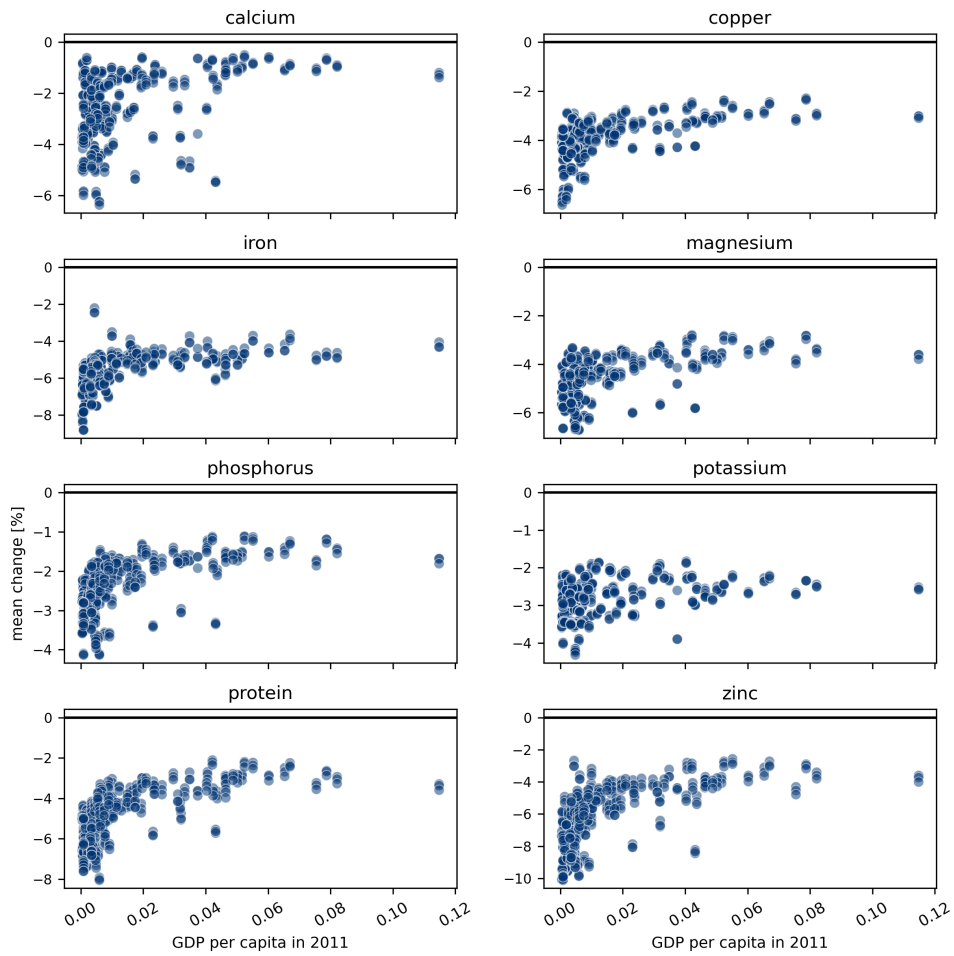


Figure B.1: Mean percent change per nutrient compared to the country's GDP per capita in 2011.

B.3 Changes in Nutritional Intake (95% Confidence Intervals)

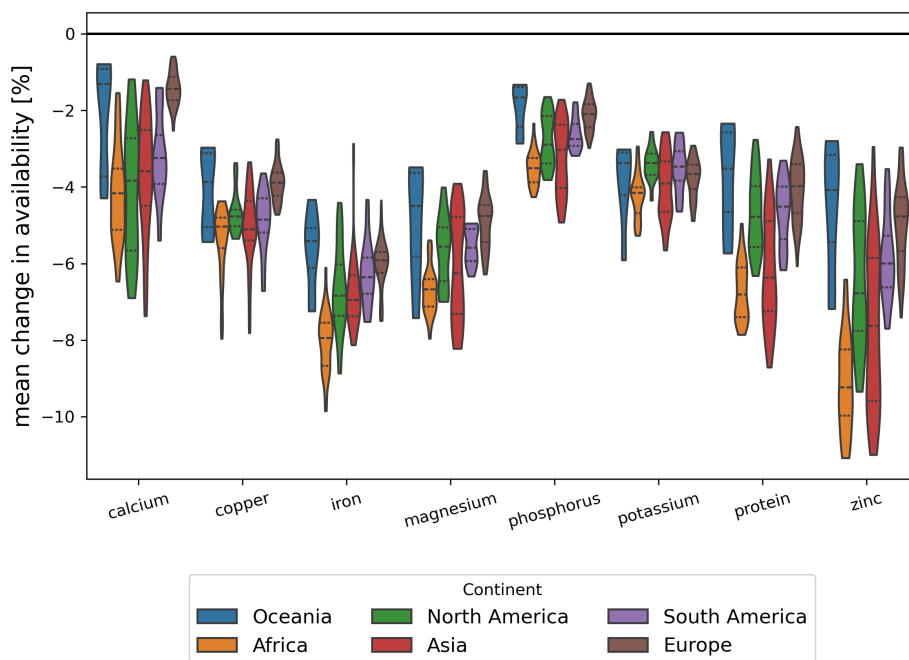


Figure B.2: Decrease in the percentage change at the 2.5% confidence interval to the nutritional availability by continent due to a CO₂ increase from 350 ppm and 550 ppm.

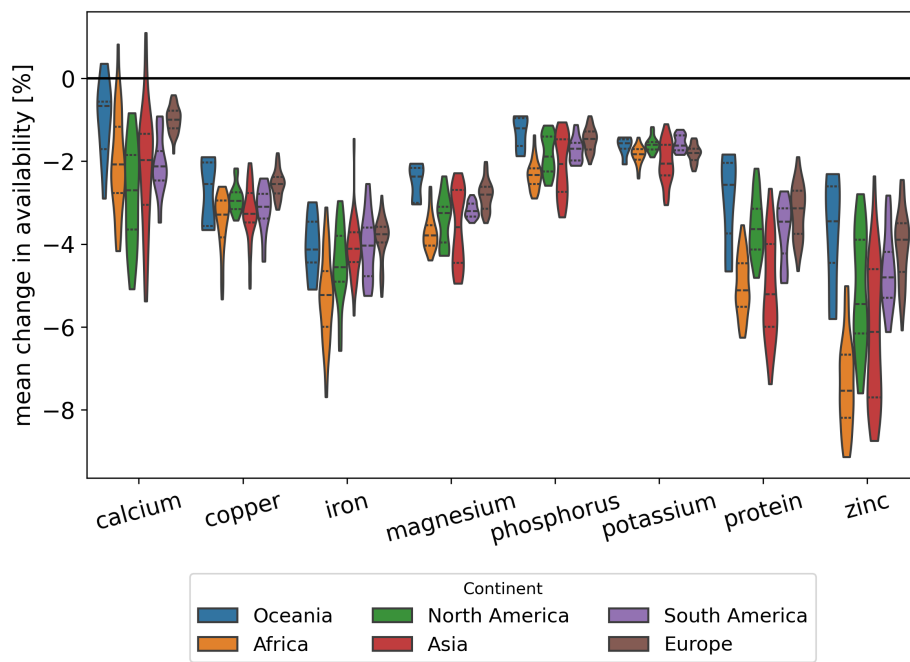


Figure B.3: Decrease in the percentage change at the 97.5% confidence interval to the nutritional availability by continent due to a CO₂ increase from 350 ppm and 550 ppm.

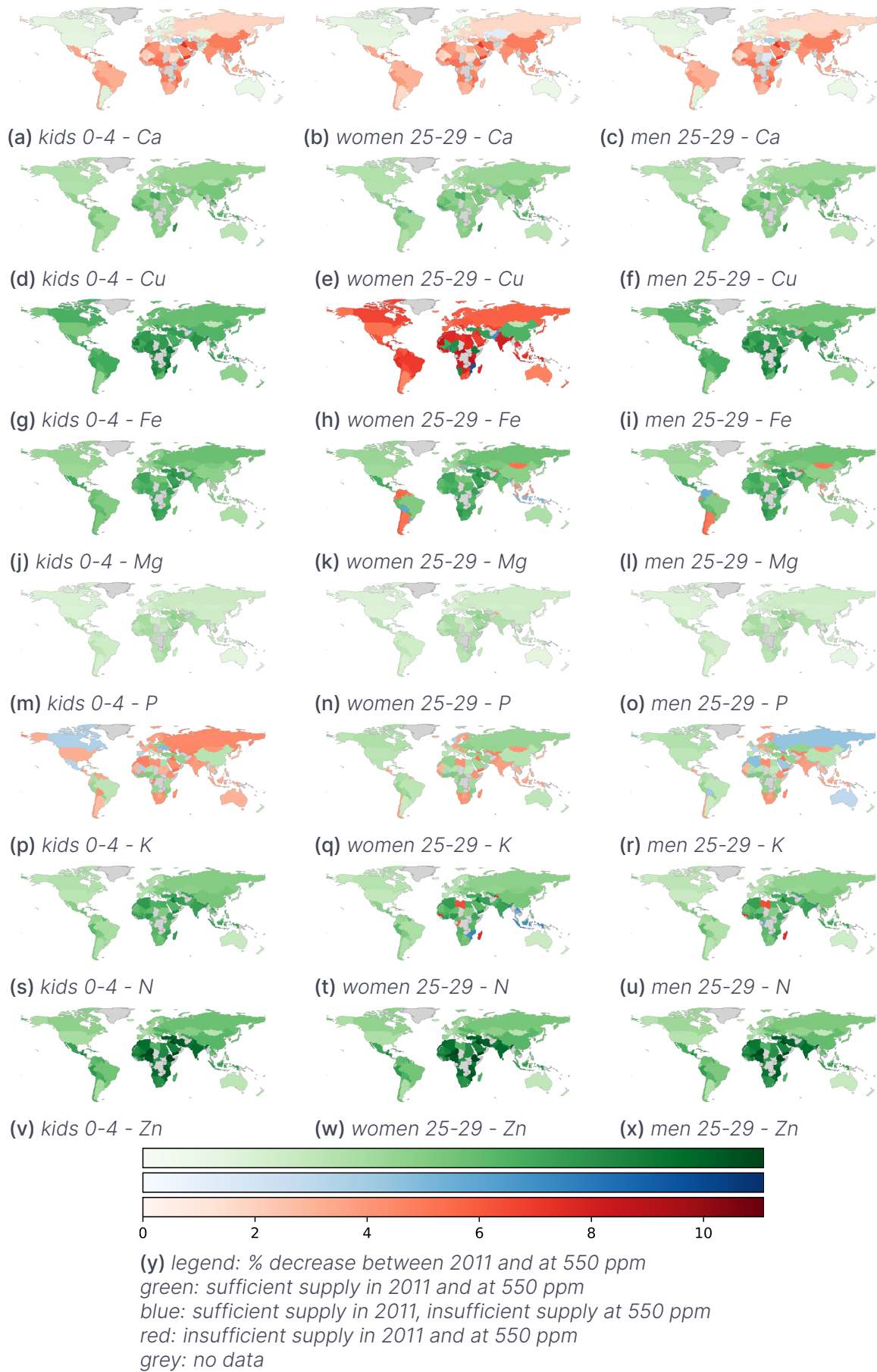


Figure B.4: 2.5% confidence interval changes in nutritional intake per element and age-sex group due to the direct effect on the plant ionome of an increase of CO₂ from 350 ppm to 550 ppm assuming the same dietary supply composition as in 2011

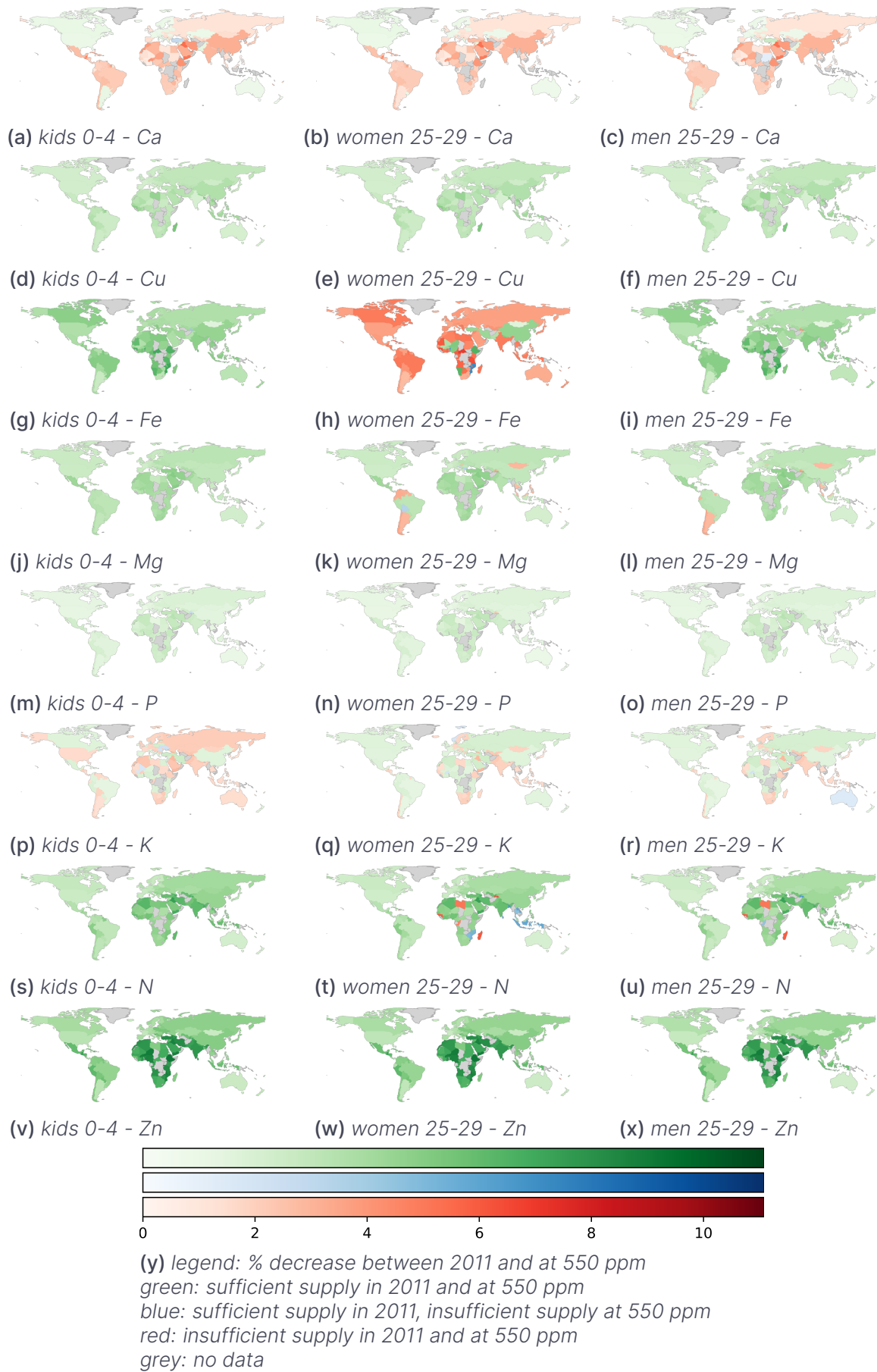
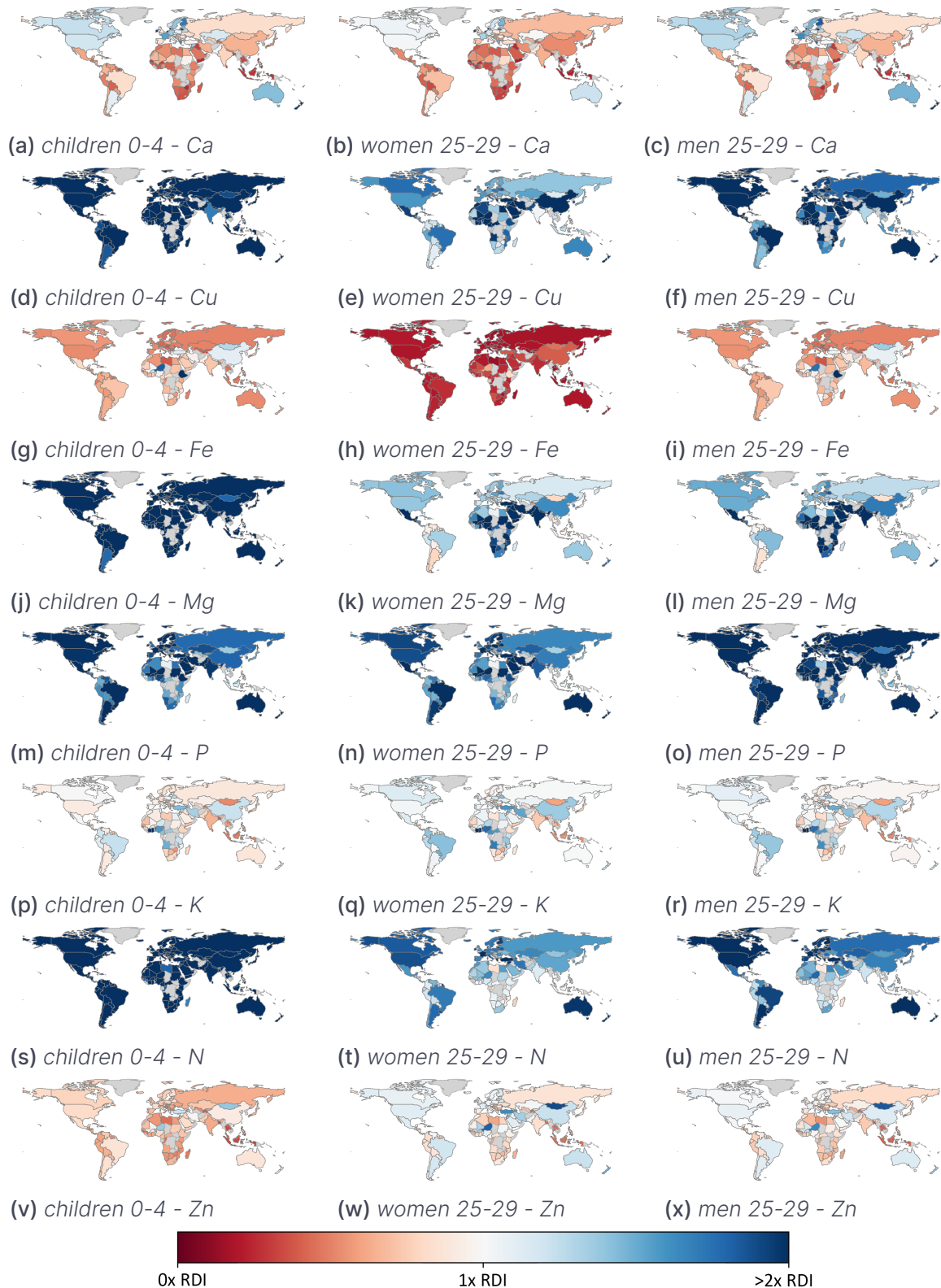


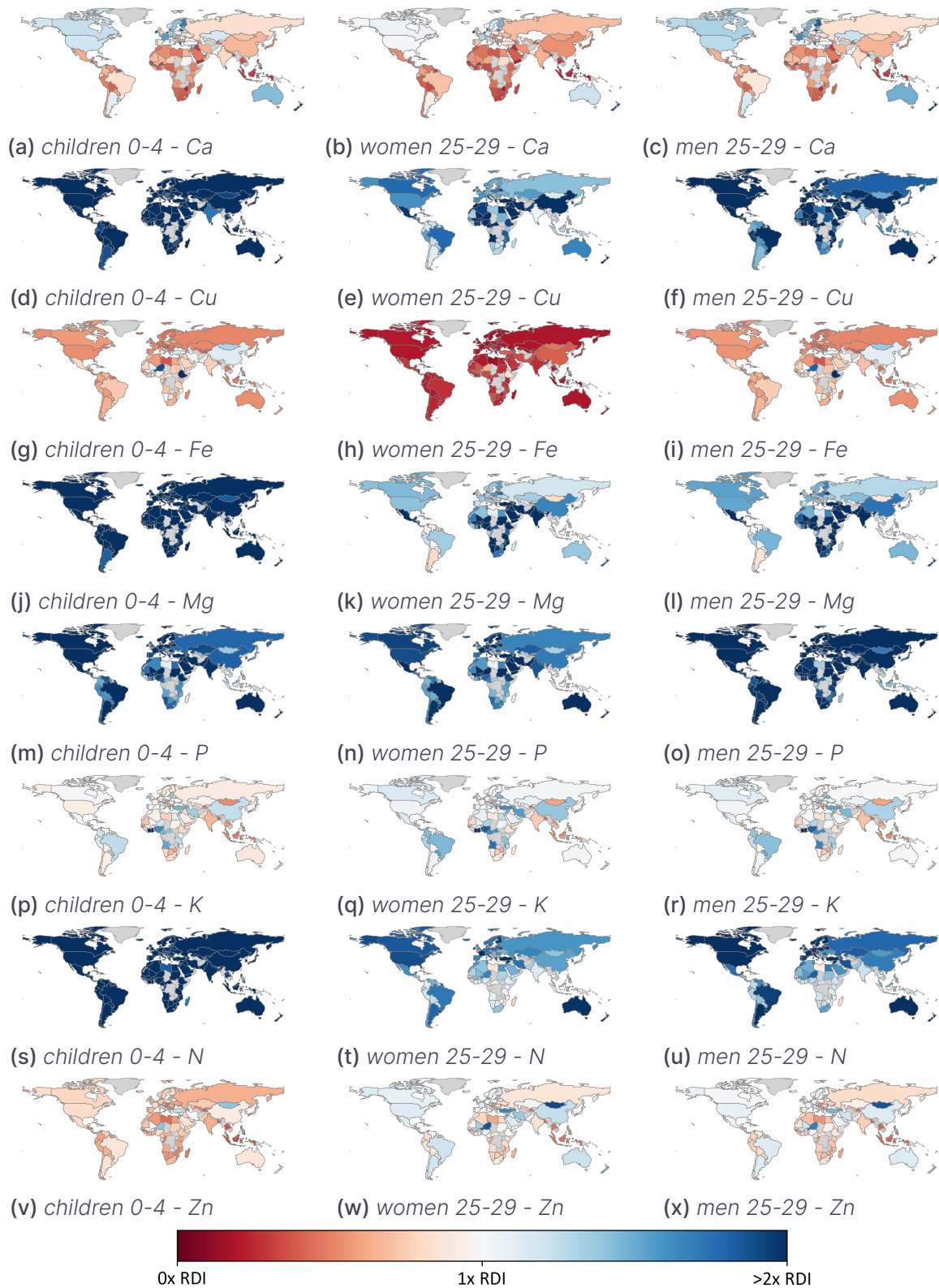
Figure B.5: 97.5% confidence interval changes in nutritional intake per element and age-sex group due to the direct effect on the plant ionome of an increase of CO₂ from 350 ppm to 550 ppm assuming the same dietary supply composition as in 2011

B.4 Malnutrition Rates at 550 ppm (95% Confidence Interval)



(y) legend: daily supplied nutrients as a ratio compared to the RDI
 grey: no data

Figure B.6: 2.5% confidence interval of the daily supply of nutrients as a ratio of the RDI in a 550 ppm world assuming the same dietary supply composition as in 2011.



(y) legend: daily supplied nutrients as a ratio compared to the RDI
 grey: no data

Figure B.7: 97.5% confidence interval of the daily supply of nutrients as a ratio of the RDI in a 550 ppm world assuming the same dietary supply composition as in 2011.